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EGG ARCHITECTURE OF NAUCORIDAE (HETEROPTERA): INTERNAL AND EXTERNAL STRUCTURE OF THE CHORION AND MICROPYLE

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Abstract.—The chorion and micropyles of 27 species of Naucoridae, including 21 species of *Ambrysus,* are described and each description is supported with scanning electron micrographs. Photomicrographs of thick sections through the chorion or micropyle of 10 of these species also are presented. Chorionic sculpturing differs interspecifically in *Ambrysus* and based on the species studied, eggs of *Ambrysus, Limnocoris,* and *Pelocoris* have 2–3 micropyles.

Key Words: Egg, chorion, micropyle, Naucoridae

The Naucoridae *(sensu lato),* or creeping water bugs, comprise 394 described species worldwide (see La Rivers 1971, 1974, 1976; Polhemus and Polhemus 1982, 1988, 1994; Nieser et al. 1993; Liu and Zheng 1994; Polhemus 1994; Nieser and Chen 1996). As is typical among insect families, the adults have received the greatest amount of morphological research; accordingly, taxonomic treatments emphasize adult characters. Although nymphal stages have been described for several species of Naucoridae, details of egg structure largely have been ignored. Line diagrams from light microscopy have been presented for a few species; however, elucidation of fine detail is not possible with this technique. Recent reports for several species [*Ambrysus lunatus* Usinger (Sites and Nichols 1990), *Cryphocricos hungerfordi* Usinger (Sites and Nichols 1993), *Pelocoris poeyi* Guérin Méneville (Sites 1991), and several species of South American *Ambrysus* and *Pelocoris* (López Ruf 1989)] have included scanning electron micrographs that have revealed interspecific differences in chorionic patterns.

Eggs of most naucorid species, for which oviposition is known, either are adhered to plants (exophytic oviposition) or to rock substrata (Hinton 1981). For example, eggs of *A. lunatus* are adhered to plants (Sites and Nichols 1990), *Ambrysus mormon* Montandon to pebbles (Usinger 1946), *Aphelocheirus aestivalis* (Fabricius) probably to rocks (Larsén 1927), *C. hungerfordi* to rocks (Sites and Nichols 1993), *Laccocoris limigenus* Stål to hard substrata (Clarke and Baroudy 1990), *Naucoris maculatus* F. to plants (Lebrun 1960), and *Pelocoris femoratus* (Palisot de Beauvois) to plants (Torre Bueno 1903, Hungerford 1927, McPherson et al. 1987). More specifically, *P. femoratus* eggs are glued to leaflets of *Nitella* and other aquatic plants with a "fairly generous quantity of white adhesive" (Hungerford 1927). In contrast, the oviposition of *Ilyocoris cimicoides* (L.) is endophytic, inserting eggs into submergent plant tissue (Cobben 1968), such as into stems of *Ranunculus* or water peppermint (Rawat 1939).

Eclosion occurs through the anterior pole and, generally, a crescentic slit is made

through the chorion. In *Coleopterocoris kleerekoperi* Hungerford and species of *Cryphocricos,* a predetermined fracture line exists, and in *I. cimicoides,* a well-defined operculum faces the water, whereas the remainder of the egg is embedded within the plant (see Rawat 1939).

Internally, the chorion of *Ilyocoris* and *Cryphocricos* is bilayered (Cobben 1968 and Sites and Nichols 1993, respectively), with a thick chorionic outer layer, which is perforated by pore canals, and a thinner, unperforated chorionic inner layer. Externally, scanning electron micrographs of six species of *Pelocoris* and two species of *Ambrysus* from Argentina revealed that the chorionic surface differed among species (López Ruf 1989). For the two species of *Ambrysus,* interspecific internal differentiation was subtle; however, marked differences existed externally. Therefore, López Ruf (1989) suggested that the external chorionic pattern is valuable as a taxonomic character and that internal chorionic attributes may be useful at the generic level.

Presented herein are scanning electron micrographs of the chorion and micropyles of 21 species of *Ambrysus* (subfamily Cryphocricinae) and selected species representing six additional genera and five additional subfamilies. Photomicrographs of thick sections of the micropyle and chorion for some species also are presented. Egg morphology is described for each species.

Materials and Methods

Eggs were obtained by both oviposition and dissection. Oviposited eggs were preferred for examination because they were fully developed structurally. Thus, we brought live female naucorids into the laboratory and maintained them individually in glass petri dishes with enough water to submerge them. To provide a potential oviposition substrate, an aquatic plant stem (usually *Justicia americana*) was placed in each petri dish and live food provided for each naucorid generally as one corixid (*Corisella, Ramphocorixa, Sigara*) per naucorid, daily. Most naucorids, including members of those species inhabiting lotic environments, oviposited on plants or on the dish. For the several species that did not oviposit in the laboratory or for which we did not have live specimens, eggs were dissected from females preserved in alcohol. Eggs were taken from only the common oviduct or vagina (sometimes erroneously referred to as ovarian eggs), rather than from the ovarioles, and were considered to be structurally well-developed because they were near the end of the reproductive tract. To allow a rapid evaluation of the reproductive tract to determine position of eggs and to minimize external damage to the specimen, a dissection technique was developed. With the insect in alcohol and ventral side up, the tip of a pair of jeweler's forceps was inserted into the membrane of the lateral margin of the 7th abdominal segment. By moving the forceps anteriorly, the sternum and laterotergites were separated from the terga of segments 4–7. The venter then was pulled laterally, separating along segmental sutures, thereby exposing the abdominal cavity. Eggs were gently removed from the abdomen with forceps and kept in 3.7 ml snap-cap glass vials in 80% ethyl alcohol.

Dissected eggs often had tissue from the reproductive tract adhered to them. To remove this tissue, an ultrasonic cleaner was used, which had a peak output of 40 watts and a frequency of 60 Hz. Vials containing eggs in ethyl alcohol were placed in the cleaner with a small amount of water for ca. 10 minutes: the exact amount of time depended on the amount of tissue to be removed. Various solublizers [e.g., Triton X-100, sodium dodecyl sulfate (SDS)] were ineffective in removing tissue. Subsequently, the eggs were examined under a microscope and any remaining tissue was carefully removed. Eggs then were transferred to fresh 80% ethyl alcohol.

To prepare eggs for critical point drying, both dissected and oviposited eggs in 80% ethyl alcohol were fixed with 2% glutaraldehyde in 0.1 M phosphate buffer, washed

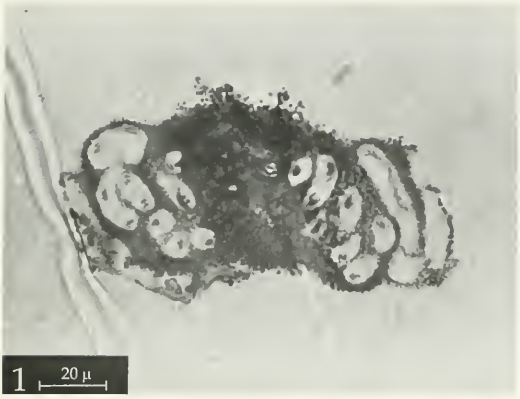


Fig. 1. *Ambrysus circumcinctus*, cross section through micropylar plug distad of base.

in 0.1 M phosphate buffer, and dehydrated through a graded alcohol series to 100% ethyl alcohol, and then placed into 100% acetone. Eggs were then critical point dried and sputter-coated. For light microscopy, the above procedure was followed through the glutaraldehyde primary fixation. After washing in 0.1 M phosphate buffer, eggs were subjected to a secondary fixation in 2% osmium tetroxide in 0.1 M phosphate buffer. Subsequent dehydration techniques were as for the scanning microscopy preparation. Eggs were embedded in Spurr's resin, sectioned with a diamond knife, slide-mounted, and stained with toluidine blue. Voucher specimens of adults and eggs are housed in the Enns Entomology Museum, University of Missouri–Columbia.

Descriptions of Eggs

Little detail of the micropylar plug of most genera is evident externally that would allow the determination of the number of micropyles contained therein. Cross sections taken at levels above the base of the plug reveal numerous canals, including transverse canals, which represent convolutions of the same canal(s) throughout the plug (Fig. 1). However, the number of micropyles can be observed by sectioning through the base of the plug where it enters the egg. Thus, photomicrographs of thick sections taken through the base of the plug are presented for some species.

Citations for the original description and subsequent descriptions of adults or immature stages are given for each species. Also given are collecting localities of females from which eggs were obtained, egg measurements (mm ± SE), sample size, and method of obtainment (i.e., oviposited or dissected). For all naucorid species examined, egg color was creamy white to beige.

Subfamily Cryphocricinae Montandon 1897a

Genus *Ambrysus* Stål 1862

Ambrysus (Acyttarus) funebris La Rivers (Figs. 2–5)

Ambrysus funebris La Rivers 1948a: 103–107.

USA: California, Death Valley National Monument

Length, 1.04; width, 0.38; n = 1; dissected.

Overall appearance elongate with rounded, asymmetrical ends. Reticulation pattern consisting generally of pentagonal to heptagonal units, delimited by distinctly raised lines (Fig. 2). Within each unit, poorly defined, low, irregular protruberances. Aeropyles small, distinct, numerous, more than 50 per unit (Fig. 3). Anterior pole with reticulation and aeropyles lacking, with amorphous micropylar plug set in shallow concavity (Fig. 4).

Exochorion thicker than endochorion. Pore canals widest at base (Fig. 5).

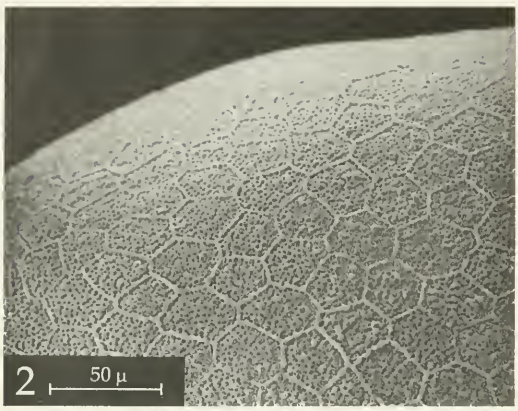
Ambrysus (Syncollus) circumcinctus Montandon (Figs. 6–9)

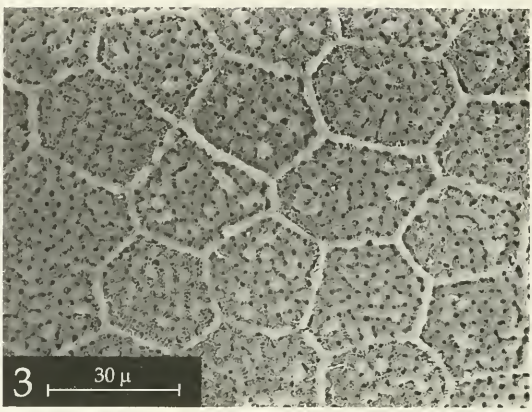
Ambrysus circumcinctus Montandon 1910: 442–444.

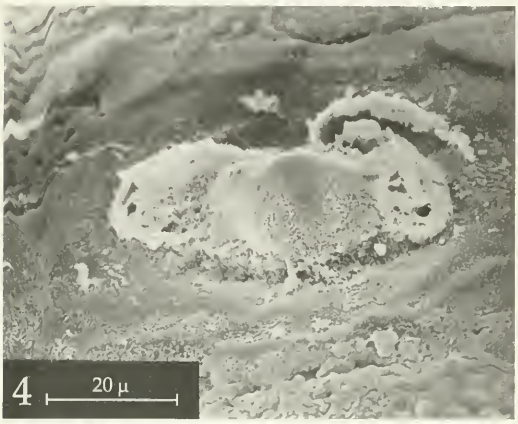
USA: Texas, Kimble Co., Junction

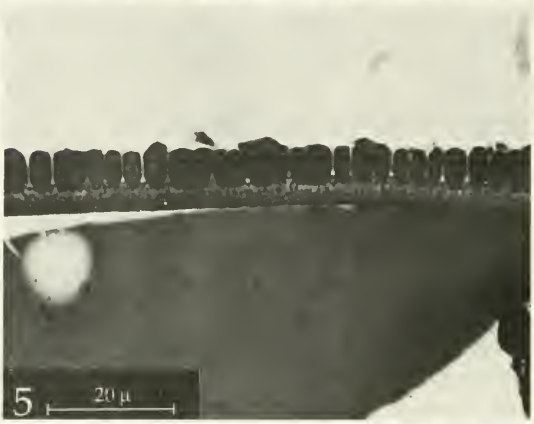
Length, 1.11 ± 0.01; width, 0.48 ± 0.01; n = 10; dissected.

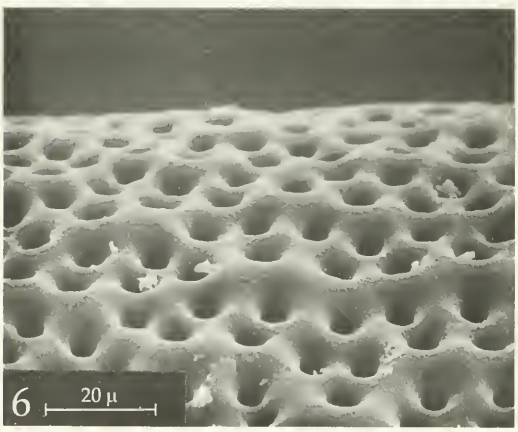
Overall appearance elongate-oval. Reticulation pattern only faintly visible as impressed lines. Within each unit formed by

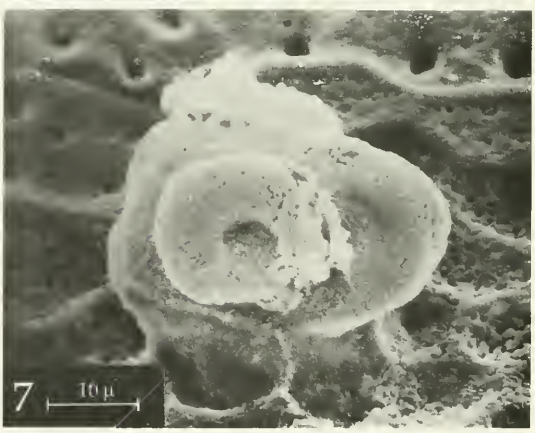








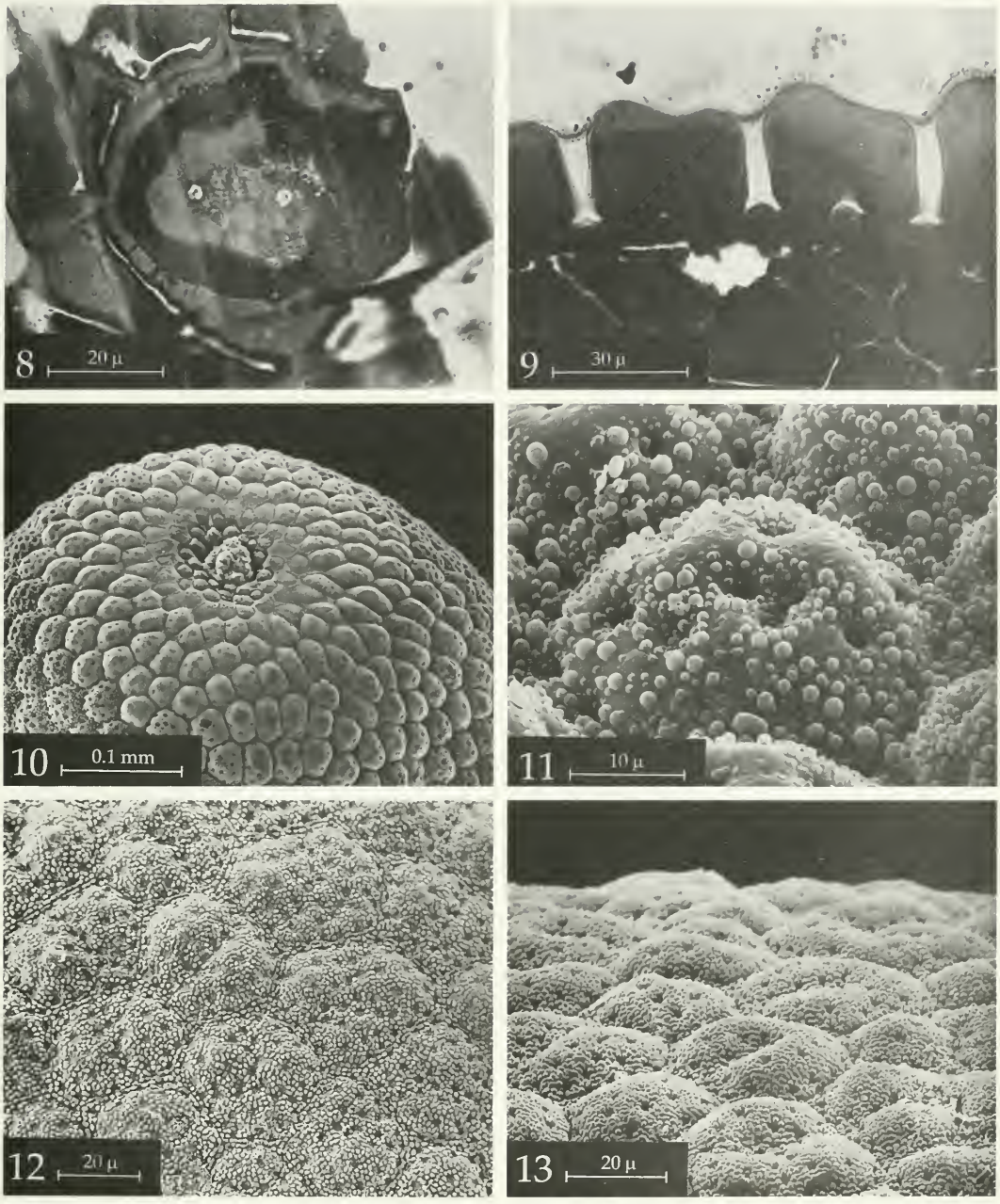




Figs. 2–7. 2–5, *Ambrysus funebris*. 2, 3, Chorion surface. 4, Micropylar plug. 5, Chorion section. 6, 7, *A. circumcinctus*. 6, Chorion surface. 7, Micropylar plug.

pattern, 5–8 aeropyles set in deep individual sockets (Fig. 6). Anterior pole with reticulation pronounced with raised lines and with aeropyles absent. Micropylar plug at anterior pole, ovate, and with two distinct, lateral helical micropylar tubes (Fig. 7). Section through base of micropylar plug with two micropyles (Fig. 8). Protuberances other than micropyle lacking.

Exochorion ca. 4 × thicker than endochorion. Pore canals widest at base (Fig.9).



Figs. 8–13. 8, 9, *Ambrysus circumcinctus*. 8, Micropyle section at base of plug. 9, Chorion section. 10, 11, *A. montandoni*. 10, Anterior pole with micropylar plug. 11, Chorion surface. 12, 13, *A. arizonus*, chorion surface.

Ambrysus (Syncollus) montandoni La Rivers
(Figs. 10, 11)

Ambrysus montandoni La Rivers 1963: 1–5.
VENEZUELA: Territorio Amazonas, Tobogan

Length, 1.34; width, 0.64; n = 1; dissected.

Overall appearance elongate-oval. Reticulation pattern generally consisting of tetragonal to heptagonal units, delimited by sulci between adjacent hemispherical, funcular mounds (Fig. 10). Within each

unit, 15–30 aeropyles, becoming less distinct toward anterior pole. Aeropyles in sulci as well as on mounds. Numerous globules adhered to surface (Fig. 11). (Although these globules may be artifacts, they were persistent even after sonication in 100% acetic acid.) Reticulation less conspicuous anteriorly because mounds become flattened until immediate vicinity of micropyle where smaller reticulation units are evident (Fig. 10). Micropylar plug at anterior pole and amorphous. Protuberances other than micropyle, mounds, and granules lacking.

Ambrysus (Ambrysus) arizonus La Rivers
(Figs. 12–15)

Ambrysus arizonus La Rivers 1951: 320–322.
USA: Arizona, Gila Co., Jakes Corner
Length, 1.45 ± 0.01; width, 0.77 ± 0.01; n = 8; oviposited.

Overall appearance elongate-oval. Reticulation generally consisting of pentagonal to heptagonal units, delimited by depressions. Each depression with double row of elongate papillae defining unit boundaries (Fig. 12). Within each unit, chorion raised and coarsely papillose (Fig. 13). Aeropyles indistinct, evident as pitted appearance among papillae; number 20–50 per cell. Tubercles lacking. Anterior pole with reticulation and papillae less distinct. Micropylar plug amorphous; section through base of micropylar plug with two micropyles (Fig. 14).

Exochorion distinctly thicker than endochorion. Pore canals widest in basal third (Fig. 15).

Ambrysus (Ambrysus) buenoi Usinger
(Figs. 16, 17)

Ambrysus buenoi Usinger 1946: 199–200.
USA: Texas, Kimble Co., Junction
Length, 1.32 ± 0.02; width, 0.65 ± 0.02; n = 11; oviposited.

Overall appearance elongate-oval. Surface comprising a series of anastomosing mounds with irregularly produced protuberances (Fig. 16). Bases of mounds with large aeropyles distributed randomly. Chorionic surface, including swells and protuberances, granular (Fig. 17). Micropyle amorphous. Chorionic surface immediately surrounding micropyle lacking regular surface features, although poorly defined mounds may occur.

Ambrysus (Ambrysus) crenulatus
Montandon
(Figs. 18, 19)

Ambrysus crenulatus Montandon 1897a: 13–14.
ECUADOR: Napo Province, Puerto Napo
Length, 1.12 ± 0.01; width, 0.49 ± 0.01; n = 10; dissected.

Overall appearance elongate-oval. Reticulation generally consisting of pentagonal to heptagonal units, delimited by distinctly raised, thin walls (Fig. 18). Each unit appearing as a deep socket, with approximately 8–17 large, irregularly distributed aeropyles (Fig. 19). Tubercles lacking. Anterior pole with reticulation less distinct. Micropylar plug amorphous. Protuberances other than micropyle and raised reticulation lacking.

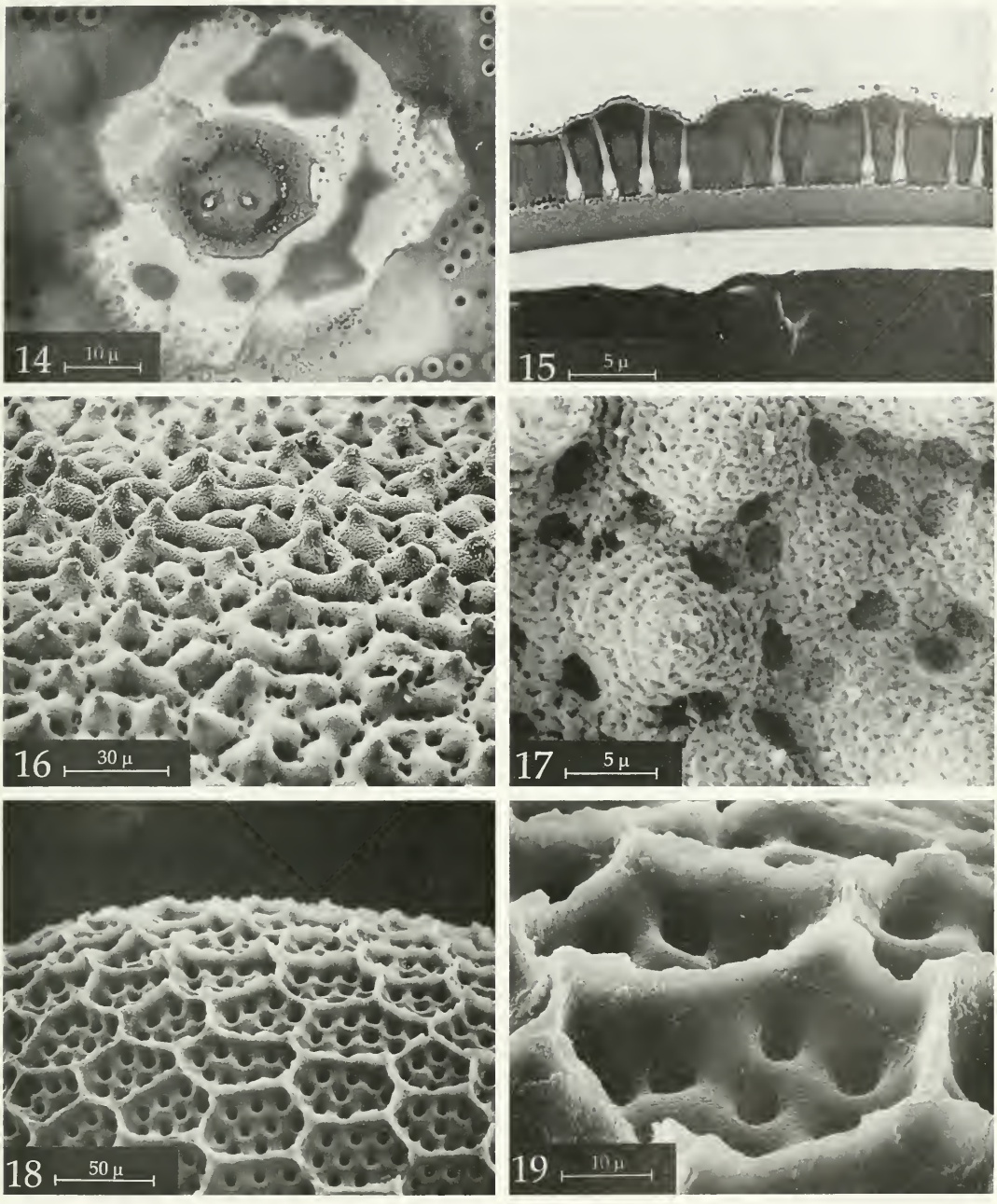
Ambrysus (Ambrysus) fossatus Usinger
(Figs. 20, 21)

Ambrysus fossatus Usinger 1946: 191–192.
ECUADOR: Napo Province, Puerto Napo
Length, 1.23 ± 0.03; width, 0.57 ± 0.02; n = 3; dissected.

Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units and only faintly visible (Fig. 20). Within each unit, 10–20 conspicuous aeropyles. Chorionic surface devoid of protruberances other than micropyle. Middle of pore canals generally parallel-sided (Fig. 21). Micropylar plug amorphous, acentric.

Ambrysus (Ambrysus) hungerfordi Usinger
(Figs. 22–25)

Ambrysus hungerfordi Usinger 1946: 192–194.

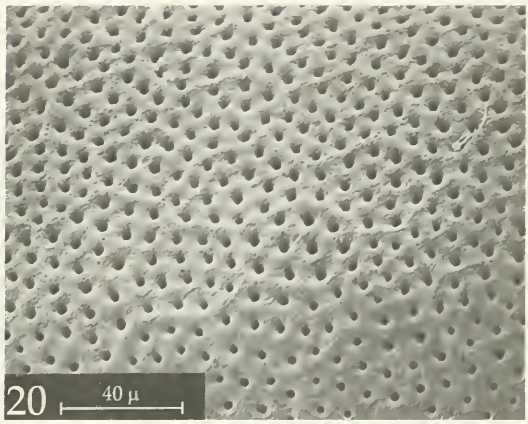


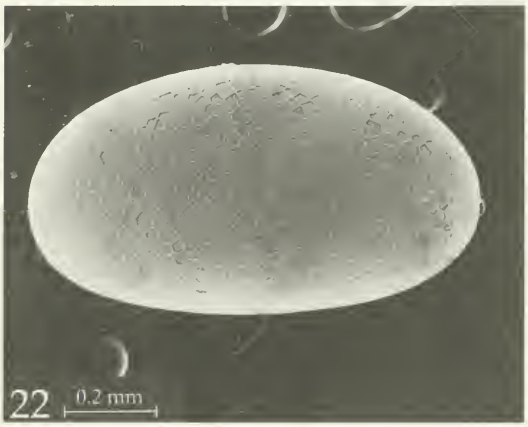
Figs. 14–19. 14, 15, *Ambrysus arizonus*. 14, micropyle section at base of plug. 15, Chorion section. 16, 17, *A. buenoi*, chorion surface. 18, 19, *A. crenulatus*, chorion surface.

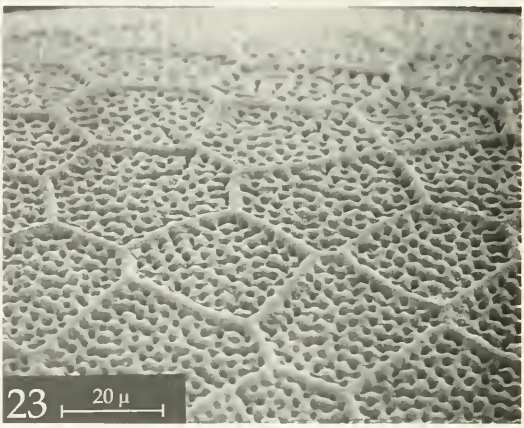
USA: Texas, Presidio Co., Big Bend Ranch State Natural Area

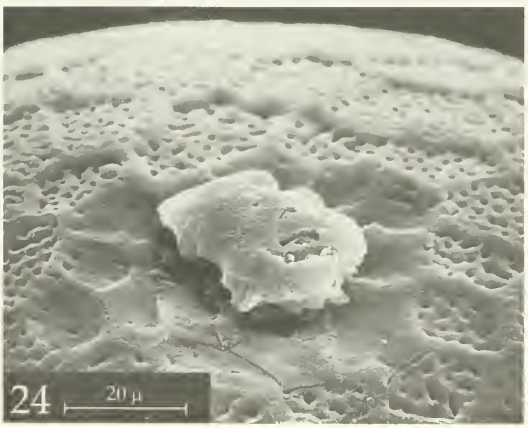
Length, 1.18 ± 0.01; width, 0.63 ± 0.01; n = 9; dissected.

Overall appearance oval (Fig. 22). Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by low, raised ridges (Fig. 23). Within each



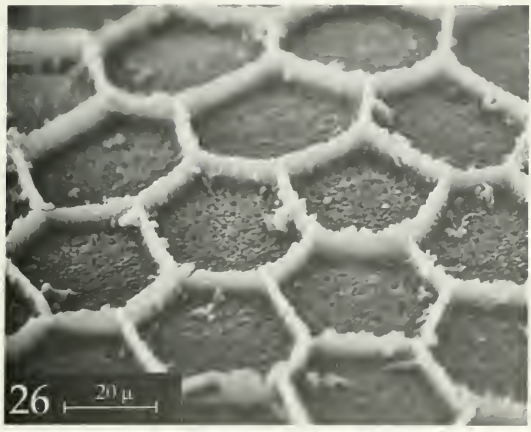


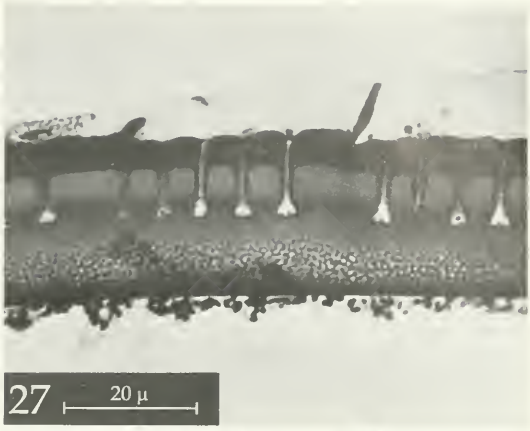


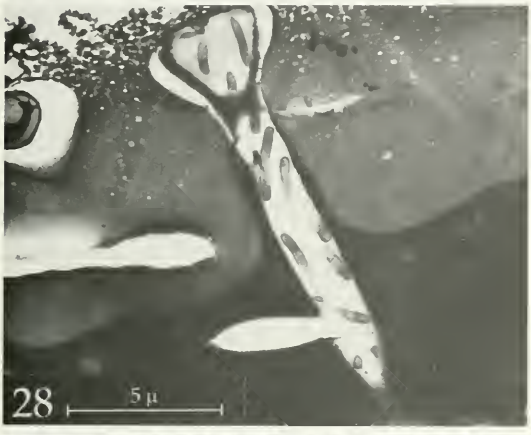


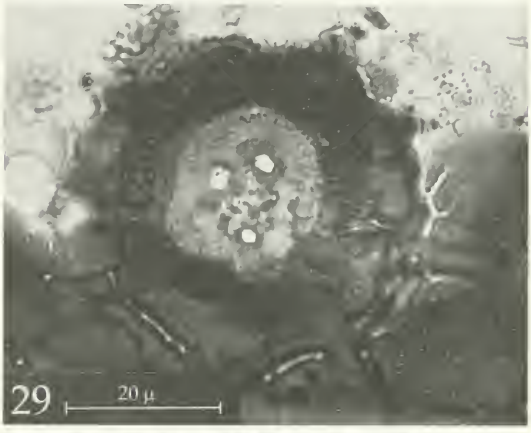
Figs. 20–25. 20, 21, *Ambrysus fossatus*. 20, Chorion surface. 21, Chorion section. 22–25, *A. hungerfordi*. 22, Whole egg. 23, Chorion surface. 24, Micropylar plug. 25, Chorion section.

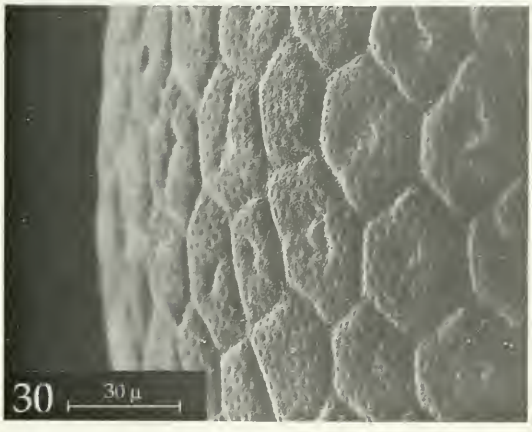
unit, 50–120 aeropyles more or less evenly distributed. Protruberances, tubercles, and papillae lacking. Micropylar plug anterior and amorphous (Fig. 24). Anterior pole with reticulation less pronounced, aeropyles fewer. Chorionic inner layer 60% as thick as chorionic outer layer (Fig. 25). Pore canals narrowest at middle.

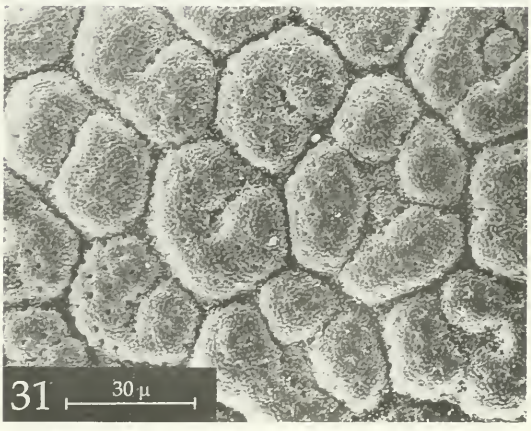












Figs. 26–31. 26, *Ambrysus inflatus*, chorion surface. 27–29, *A. lunatus*. 27, Chorion section. 28, Pore canal containing bacteria. 29, Micropyle section at base of plug. 30, 31, *A. mormon*, chorion surface.

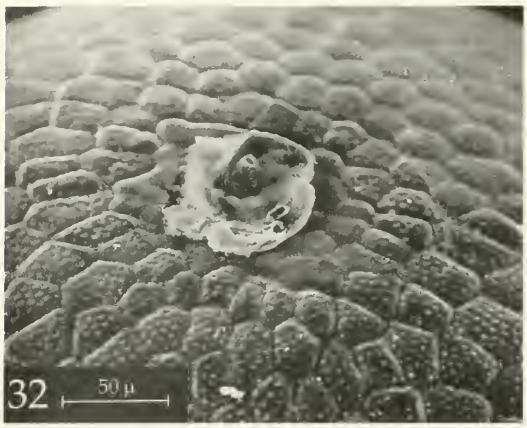
Ambrysus (Ambrysus) inflatus La Rivers (Fig. 26)

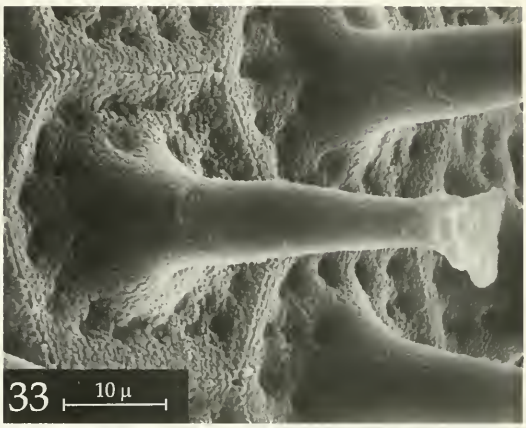
Ambrysus inflatus La Rivers 1953a: 1316–1318.

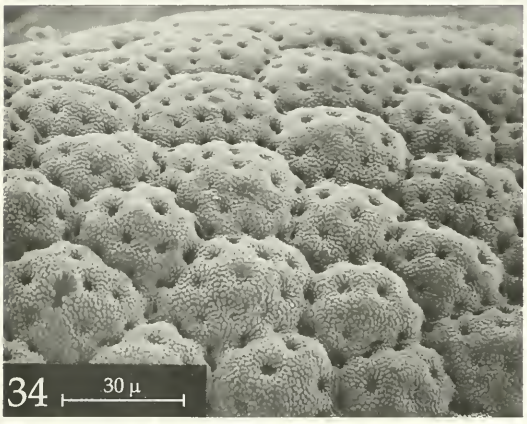
MEXICO: Jalisco, Chapala

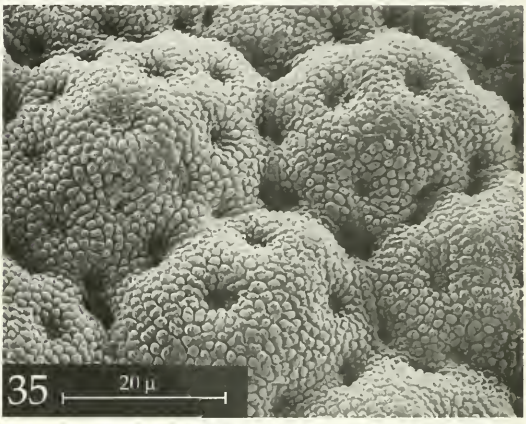
Length, 1.37 ± 0.01; width, 0.68 ± 0.01; n = 10; dissected.

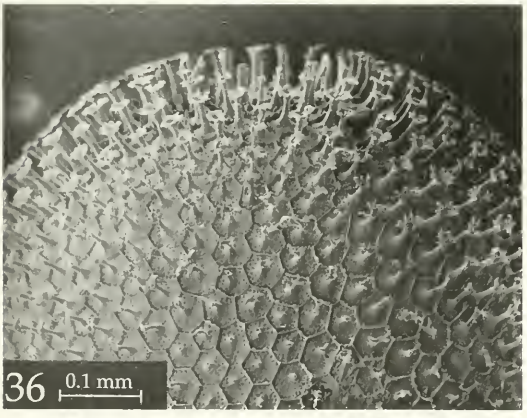
Overall appearance elongate with rounded ends. Reticulation pattern generally consisting of pentagonal to heptago-

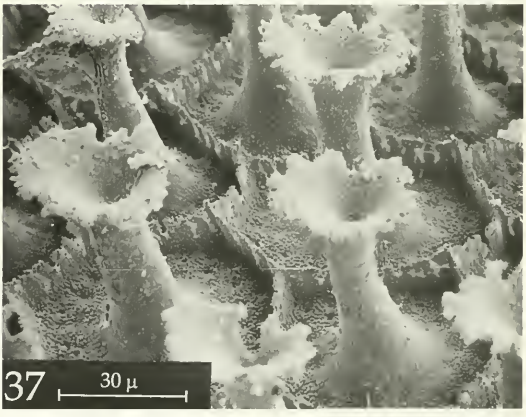












Figs. 32–37. 32, *Ambrysus mormon*, anterior pole with micropylar plug. 33, *A. occidentalis*, chorion surface with antheform processes. 34, 35, *A. plautus*, chorion surface. 36, 37, *A. portheo*. 36, Anterior pole. 37, Chorion surface with antheform processes.

nal units, delimited by a series of irregularly raised ridges with numerous tiny papillae between (Fig. 26). Scattered groups of papillae depressed, creating pitted appearance. Anterior pole with amorphous micropylar plug, without raised reticulation or papillae.

The appearance of the chorion is virtually indistinguishable from that of *A. lunatus* Usinger (see Sites and Nichols 1990).

Ambrysus (Ambrysus) lunatus Usinger
(Figs. 27–29)

Ambrysus lunatus Usinger 1946: 203–205.
Ambrysus lunatus: Sites and Nichols 1990: 800–808.
USA: Texas, Kimble Co., Junction

Endochorion subequal to exochorion in thickness (Fig. 27). Pore canals parallel-sided and widest at base. Presence of bacteria in pore canals as detected by transmission electron microscopy (Fig. 28). Micropylar plug with three micropyles (Fig. 29).

Original description of egg was given by Sites and Nichols (1990).

Ambrysus (Ambrysus) mormon Montandon
(Figs. 30–32)

Ambrysus mormon Montandon 1909: 48–49.
Ambrysus mormon: Usinger 1946: 186–187, Plate X.
USA: New Mexico, Lincoln Co., Hondo
Length, 1.70 ± 0.03; width, 0.98 ± 0.02; n = 6; oviposited.

Overall appearance elongate-oval. Reticulation pattern generally consisting of tetragonal to heptagonal units, delimited by a series of depressions between composite tumescences (Fig. 30). Tumescences rarely entire, usually completely or incompletely divided into two to four components, occasionally with a smaller, central tumescence or depression (Fig. 31). Tumescences, depressions, including reticulation, covered with papillae. Aeropyles generally distributed, neither clustered nor concentrated. Tumescences becoming flatter and less divided toward anterior pole. Micropylar plug amorphous, acentric (Fig. 32).

Usinger (1946) indicated that eggs are glued to the surface of pebbles and are suboval with a buttonlike micropyle at the anterior pole.

Ambrysus (Ambrysus) occidentalis La Rivers
(Fig. 33)

Ambrysus occidentalis La Rivers 1951: 322–325.
USA: Arizona, Gila Co., Jakes Corner
Length, 1.28 ± 0.01; width, 0.62 ± 0.00; n = 3; dissected.

Overall appearance elongate-oval. Reticulation pattern generally consisting of hexagonal units, delimited by raised boundaries. Single antheform process extending outward from center of each unit, distal end concave and expanded (Fig. 33). Margins surrounding distal concavity irregular, never in contact with adjacent antheform process. Base of antheform process widest, gradually narrowing distally. Papillae covering surface from raised reticulation to base of antheform process. 25–40 irregularly distributed aeropyles distinctly visible around base of antheform process. Anterior pole with micropylar plug, with pattern less distinct, antheform processes and papillae absent.

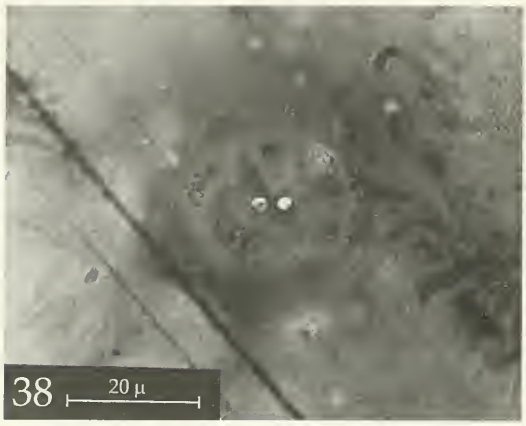
Ambrysus (Ambrysus) plautus Polhemus and Polhemus
(Figs. 34, 35)

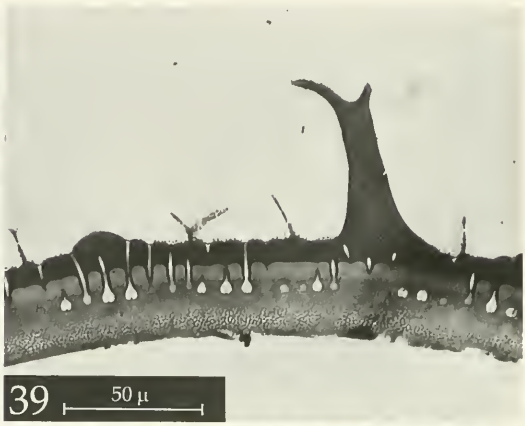
Ambrysus plautus Polhemus and Polhemus 1982: 326–328.
MEXICO: Chihuahua, Cusarare
Length, 1.12 ± 0.01; width, 0.54 ± 0.02; n = 3; dissected.

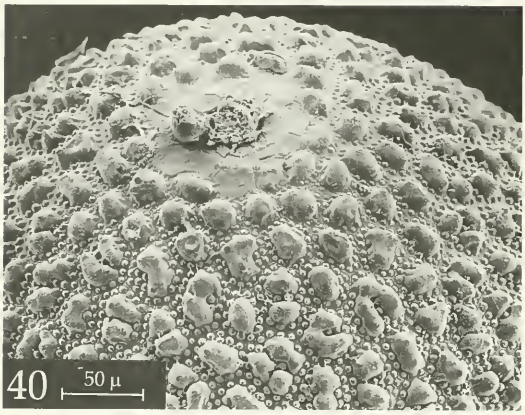
Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by depressed lines. Within each unit, chorion raised and distinctly papillose (Fig. 34). Aeropyles large, distinct; number 3–12 in interior of unit, 10–18 in depressed perimeter of unit (Fig. 35). Tubercles lacking. Anterior pole with pattern and papillae less distinct. Micropylar plug amorphous.

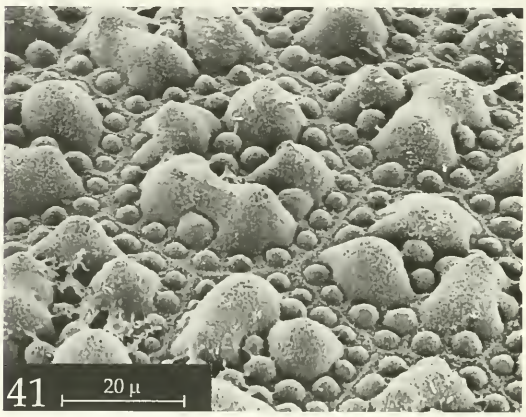
Ambrysus (Ambrysus) portheo La Rivers
(Figs. 36–39)

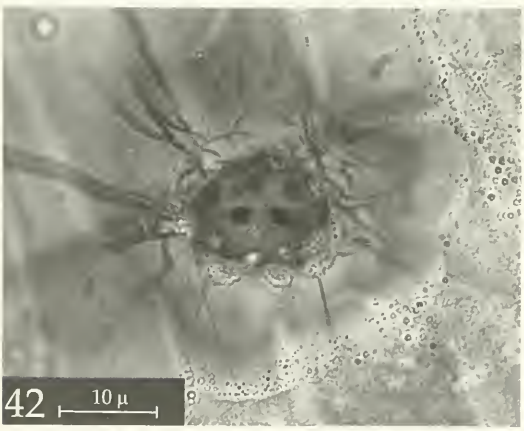
Ambrysus portheo La Rivers 1953a: 1320–1321.
MEXICO: Nuevo Leon, La Nogalera
Length, 1.56 ± 0.02; width, 0.89 ± 0.01; n = 2; oviposited.

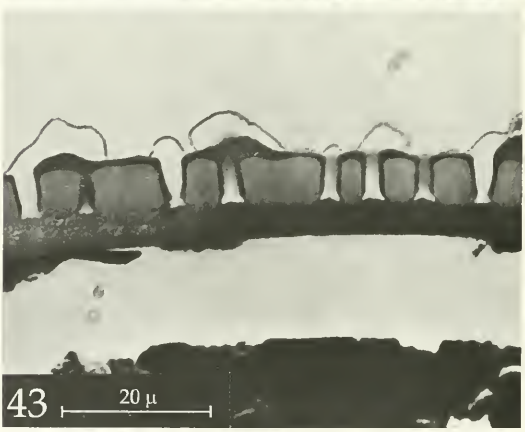












Figs. 38–43. 38, 39, *Ambrysus portheo*. 38, Micropyle section at base of plug. 39, Chorion section. 40–43, *A. pudicus*. 40, Anterior pole with micropylar plug (dislodged). 41, Chorion surface. 42, Micropyle section at base of plug. 43, Chorion section.

General appearance robust with apices slightly truncate (Fig. 36). Reticulation pattern generally consisting of pentagonal to hexagonal units, delimited by raised, fence-like boundaries. Ectal edge of boundary with irregularly-spaced, deep notches extending ca. $\frac{1}{5}$ distance to base. Single antheform process extending outward from center of each unit, the distal end of which is concave and expanded

(Fig. 37). Margins surrounding distal concavity irregular, never in contact with adjacent antheform process. Base of antheform process widest, gradually narrowing distally. Papillae covering surface between unit boundaries and base of antheform process. Irregularly spaced aeropyles occasionally visible in gaps between papillae. Anterior pole with pattern reduced around micropylar plug, antheform processes and papillae absent. Micropylar plug with two micropyles (Fig. 38)

Exochorion slightly thicker than endochorion. Pore canals bulbous at base. Antheform processes solid, without ducts (Fig. 39).

Ambrysus (Ambrysus) pudicus Stål
(Figs. 40–43)

Ambrysus pudicus Stål 1862: 460.
USA: Texas, Kimble Co., Junction
Length, 1.12 ± 0.01; width, 0.61 ± 0.01; n = 11; oviposited.

Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by slightly raised boundaries (Fig. 40). Within each unit, protuberances of two sizes: larger tubercles and smaller pustules (Fig. 41). Perimeter of each unit with a series of ca. 12–25 pustules; additional pustules usually near center of unit and among tubercles. Tubercles number 1–5 per unit and situated near center, occasionally surrounding one or more pustules. Outline of pustules round, of tubercles amoebiform. Anterior pole with pattern faintly visible, protuberances other than micropyle lacking. Micropylar plug amorphous, acentric, with two micropyles (Fig. 42).

Exochorion thicker than endochorion (Fig. 43). Pore canals wide, ca. 0.4 × length.

Ambrysus (Ambrysus) pulchellus Montandon
(Figs. 44, 45)

Ambrysus pulchellus Montandon 1897a: 16.
USA: Texas, Kimble Co., Junction
Length, 1.36 ± 0.02; width, 0.65 ± 0.01; n = 11; oviposited.

General appearance elongate-oval with rounded apices. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by sulci between tumescences (Fig. 44). Each tumescence extends around perimeter of unit and abuts adjacent tumescences (Fig. 45). Single, smaller, irregularly-shaped tumescence within each perimeter tumescence. Occasionally, central tumescence absent, replaced by depression near center. Tumescences generally glabrous. Clusters of approximately 12–20 aeropyles distributed over surface of tumescences, concentrated near margins. Micropylar plug slightly acentric and amorphous.

Ambrysus (Ambrysus) puncticollis Stål
(Figs. 46–48)

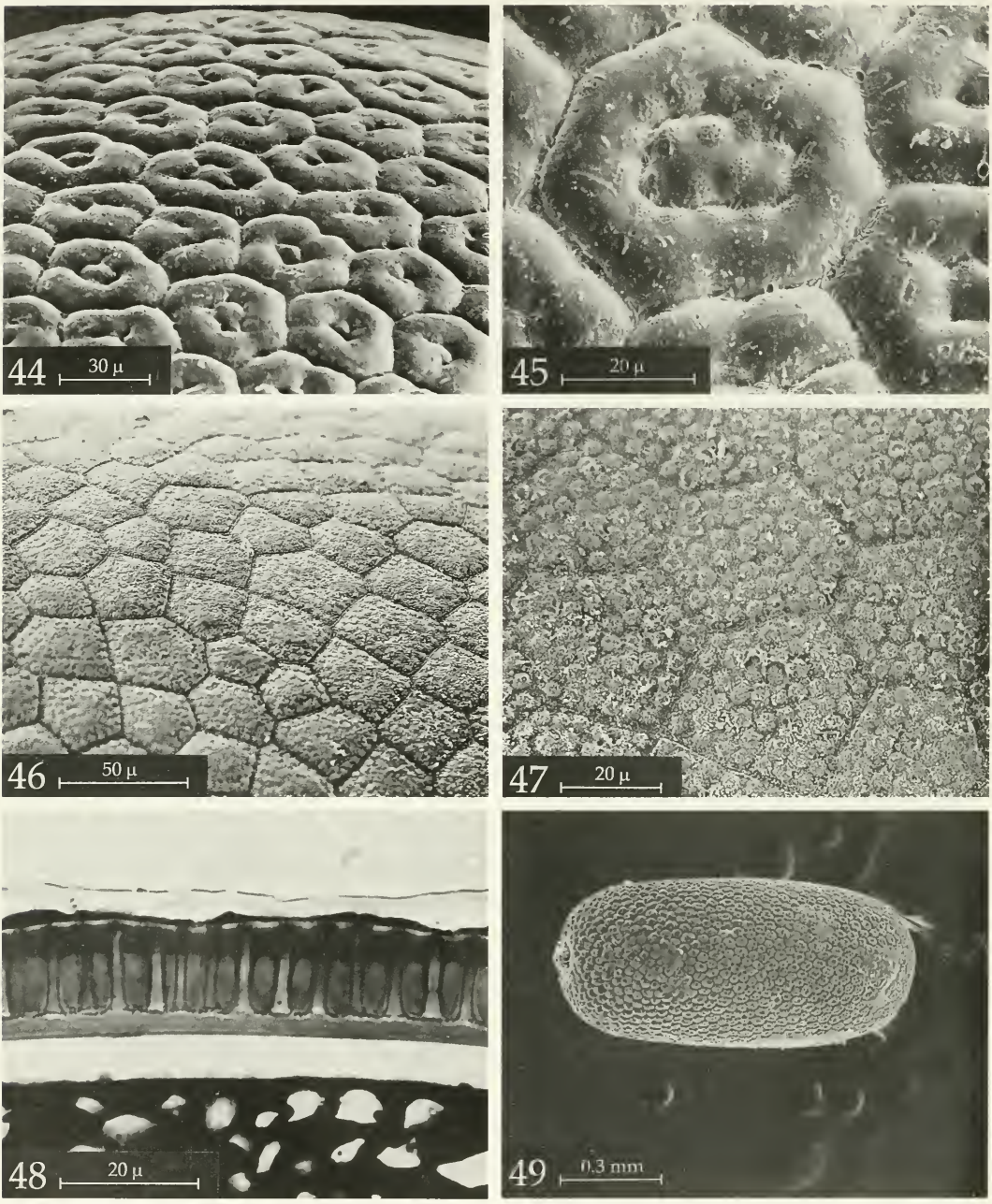
Ambrysus puncticollis Stål 1876: 143.
USA: Texas, Kimble Co., Junction
Length, 1.36 ± 0.01; width, 0.66 ± 0.01; n = 11; oviposited.

Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by depressed lines (Fig. 46). Within each unit, 20–80 large aeropyles (aeropyles filled with debris in SEMs) (Fig. 47). Protruberances, tubercles, and papillae lacking. Micropylar plug anterior and amorphous. Anterior pole with pattern less distinct.

Exochorion ca. 4.5× thicker than endochorion (Fig. 48). Pore canals slightly divergent entally and occur at somewhat regular interval.

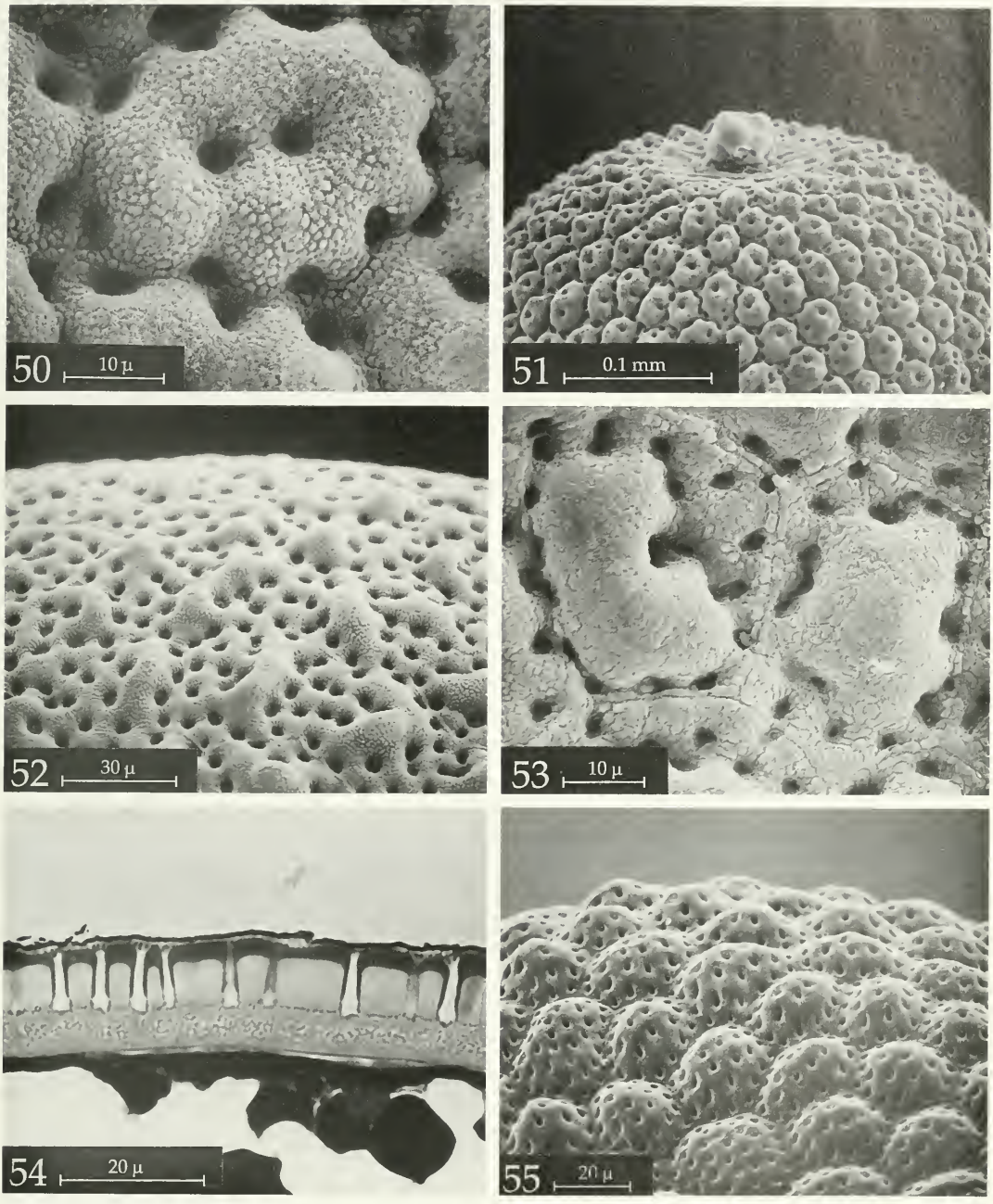
Ambrysus (Ambrysus) spiculus Polhemus and Polhemus
(Figs. 49–51)

Ambrysus spiculus Polhemus and Polhemus 1981: 400–401.
MEXICO: Chihuahua, Rio Concheño
Length, 1.10 ± 0.01; width, 0.48 ± 0.03; n = 3; dissected.



Figs. 44–49. 44, 45, *Ambrysus pulchellus*, chorion surface. 46–48, *A. puncticollis*. 46, 47, Chorion surface. 48, Chorion section. 49, *A. spiculus*, whole egg.

Overall appearance elongate-oval (Fig. 49). Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by depressed boundaries. Within each unit, chorion raised and finely papillose (Fig. 50). Perimeter of each unit with 8–16 large, distinct aeropyles; near the center of unit 1–4 aeropyles. Anterior pole with reticulation and papillae less evident. Micropylar plug amorphous (Fig. 51).



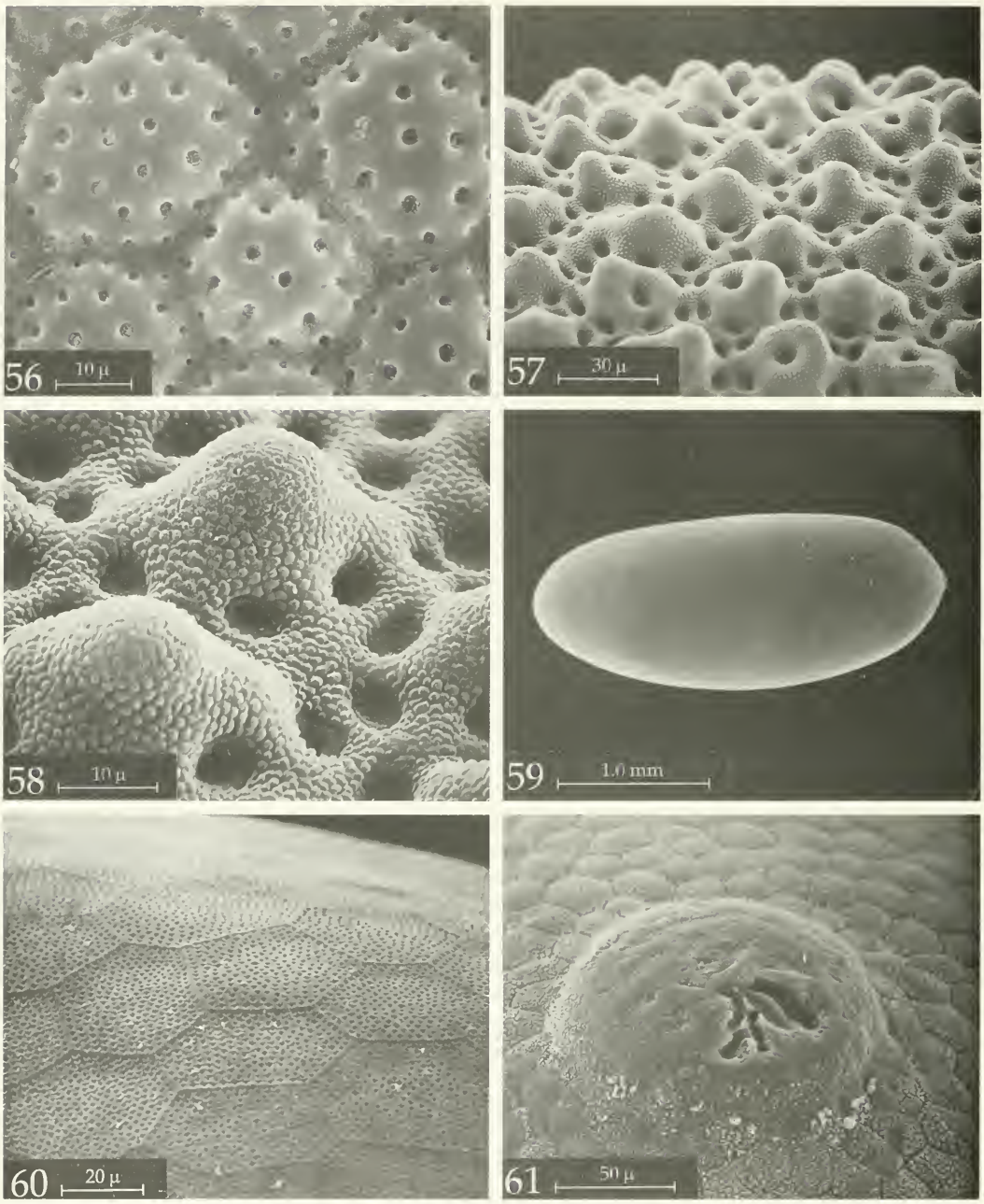
Figs. 50–55. 50, 51, *Ambrysus spiculus*. 50, Chorion surface. 51, Anterior pole with micropylar plug. 52–54, *A. thermarum*. 52, 53, Chorion surface. 54, Chorion section. 55, *A. tridentatus*, chorion surface.

Ambrysus (Ambrysus) thermarum La Rivers
(Figs. 52–54)

Ambrysus thermarum La Rivers 1953b: 1–3. USA: New Mexico, Taos Co., Arroyo Hondo

Length, 1.43 ± 0.06; width, 0.72 ± 0.02; n = 10; oviposited.

Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by



Figs. 56–61. 56, *Ambrysus tridentatus*, chorion surface. 57, 58, *A. woodburyi*, chorion surface. 59–61, *Gestroiella limnocoroides*. 59, Whole egg. 60, Chorion surface. 61, Micropylar plug.

double row of rounded to elongate papillae (Fig. 52). Chorionic surface generally covered with papillae. Within each unit formed by reticulation, a single amorphous tumescence (Fig. 53). Aeropyles distinct and randomly distributed on chorion except on tumescence; number 15–30 per unit. Pattern, tumescences, papillae, aeropyles becoming

less distinct toward anterior pole. Micropylar plug amorphous.

Exochorion slightly thicker than endochorion (Fig. 54). Pore canals widest at base.

Ambrysus (Ambrysus) tridentatus La Rivers
(Figs. 55, 56)

Ambrysus tridentata La Rivers 1962: 129–132.

MEXICO: Nuevo Leon, Potrero Redondo
Length, 1.14; width, 0.58; n = 1; dissected.

Overall appearance elongate-oval. Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by depressed boundaries. Chorion domed within each unit (Fig. 55). Aeropyles subcircular near center of dome, ellipsoid off-center; 20–40 per cell. Chorion smooth; papillae and tubercles lacking (Fig. 56). Anterior pole with domes diminishing in size, aeropyles becoming less evident. Micropylar plug amorphous.

Ambrysus (Ambrysus) woodburyi Usinger
(Figs. 57, 58)

Ambrysus woodburyi Usinger 1946: 194–195.

USA: Arizona, Cochise Co., Portal
Length, 1.16 ± 0.02; width, 0.57 ± 0.02; n = 10; oviposited.

Overall appearance elongate-oval. Reticulation pattern generally poorly-defined. Within each unit formed by reticulation, a single amorphous tumescence (Fig. 57). Each unit with approximately 7–12 large, distinct aeropyles randomly distributed around the tumescence. Chorionic surface generally finely papillose (Fig. 58). Anterior pole with tumescences and papillae less developed. Micropylar plug amorphous, acentric.

Subfamily Cheirochelinae Montandon 1897b
Genus *Gestroiella* Montandon 1897b
Gestroiella limnocoroides Montandon
(Figs. 59–61)

Gestroiella limnocoroides Montandon 1897b: 371–372.

THAILAND: Chiang Mai Prov., Chiang Mai
Length, 3.04 ± 0.02; width, 1.35 ± 0.02; n = 4; dissected.

Overall appearance elliptical with poles slightly acuminate (Fig. 59). Reticulation pattern generally consisting of pentagonal to octagonal units, delimited by low, elevated ridges (Fig. 60). Within each unit, 300–800 aeropyles. Micropyles incorporated into low, broad mound at anterior pole (Fig. 61). Other than micropyle, protruberances, tubercles, and papillae lacking.

Subfamily Aphelocheirinae Fieber 1851
Genus *Aphelocheirus* Westwood 1833
Aphelocheirus femoratus Polhemus and Polhemus
(Figs. 62–64)

Aphelocheirus femoratus Polhemus and Polhemus 1988: 214–216.

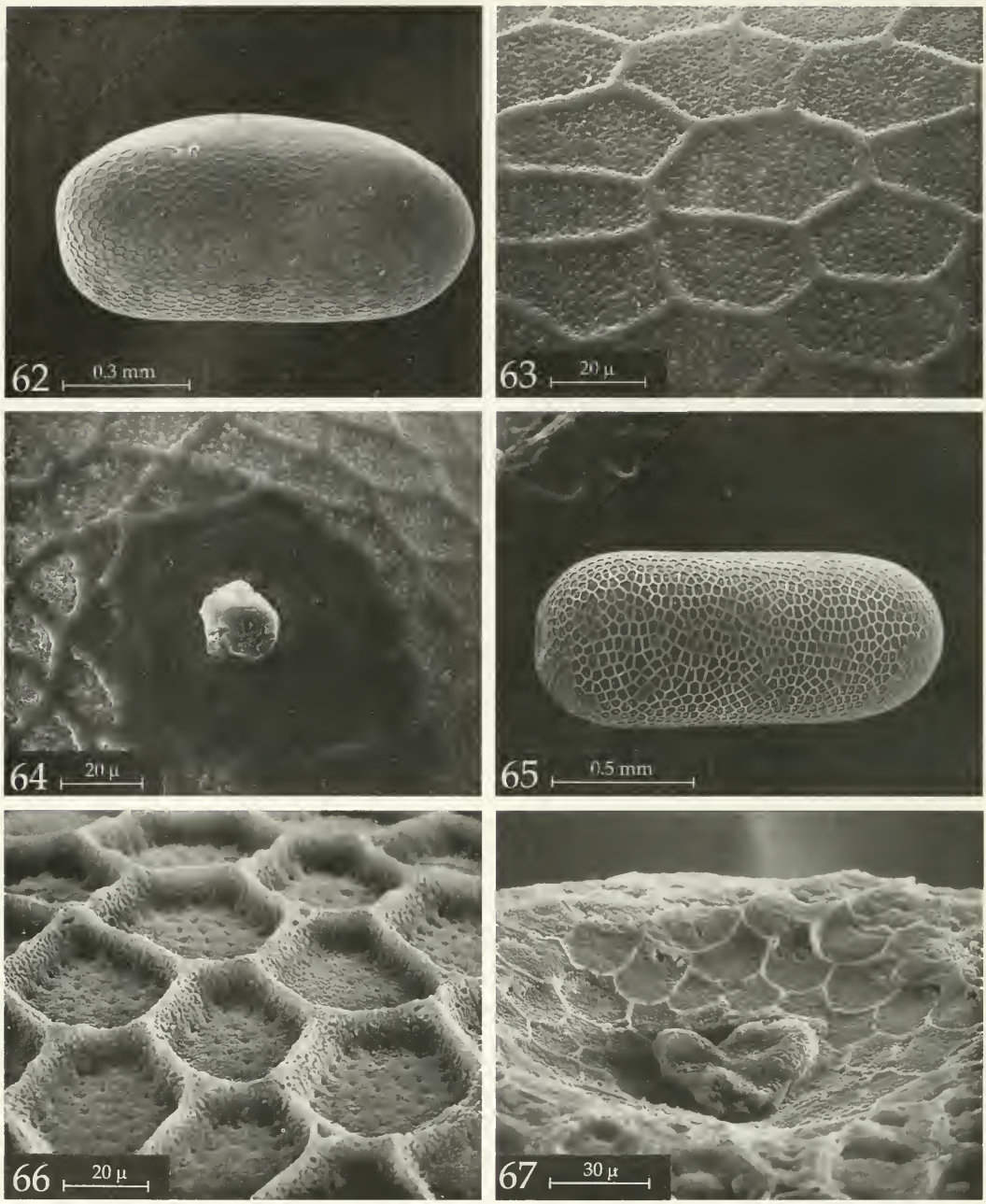
THAILAND: Songkhla Prov., Ton Nga Chang National Park
Length, 1.13 ± 0.01; width, 0.51 ± 0.01; n = 10; dissected.

General appearance oval and robust with anterior pole slightly truncate (Fig. 62). Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by broad, slightly elevated ridges (Fig. 63). Within each unit, 100–300 aeropyles. Micropyle amorphous (Fig. 64). Chorionic surface immediately surrounding micropyle lacking well-defined surface features. Other than micropyle, protruberances, tubercles, and papillae lacking.

Subfamily Laccocorinae Stål 1876
Genus *Heleocoris* Stål 1876
Heleocoris ovatus Montandon
(Figs. 65–67)

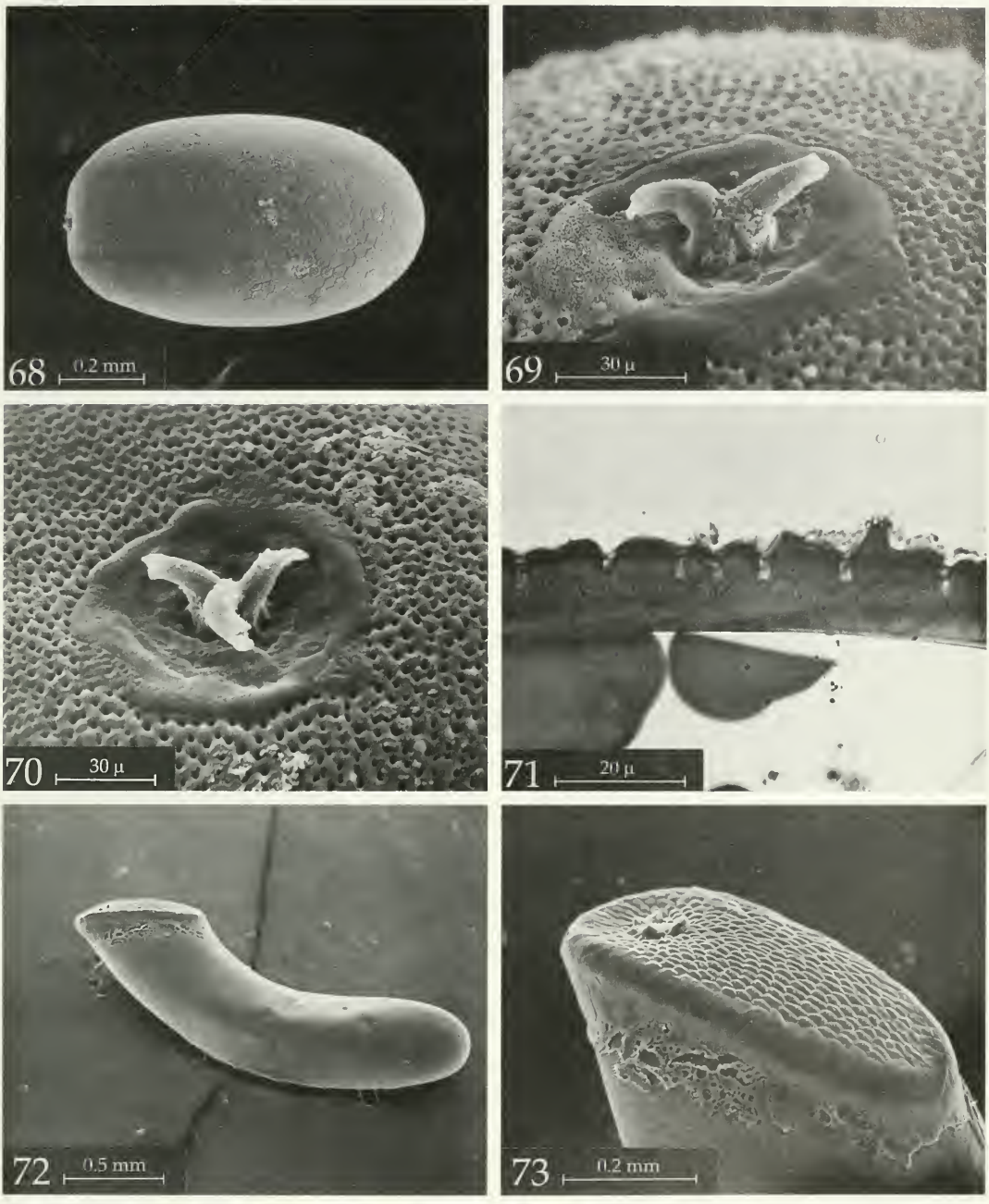
Heleocoris ovatus Montandon 1897c: 451–452.

THAILAND: Yala Province, Than To, Banglang National Park
Length, 1.55 ± 0.01; width, 0.71 ± 0.01; n = 9; dissected.



Figs. 62–67. 62–64, *Aphelocheirus femoratus*. 62, Whole egg. 63, Chorion surface. 64, Anterior pole with micropylar plug. 65–67, *Heleocoris ovatus*. 65, Whole egg. 66, Chorion surface. 67, Micropylar plug in concavity at anterior pole.

Overall appearance elongate, parallel-sided with rounded ends (Fig. 65). Reticulation pattern generally consisting of tetragonal to heptagonal units, delimited by costiform ridges (Fig. 66). Within each unit, 25–75 aeropyles. Chorionic surface generally granular. Anterior pole with amorphous micropylar plug set in acetabular depression



Figs. 68–73. 68–71, *Limnocoris moapensis*. 68, Whole egg. 69, 70, Micropyles. 71, Chorion section. 72, 73, *Ilyocoris cimicoides*. 72, Whole egg. 73, Anterior pole.

(Fig. 67). Pattern in depression becoming indistinct toward micropyle.

Pending taxonomic revision, this species has been determined probably to be *H. ovatus*. Locality and ecological data associated with the collection of the adults from which eggs were obtained are available in Sites et al. (1997).

Subfamily Limnocorinae Stål 1876
Genus *Limnocoris* Stål 1858
Limnocoris moapensis (La Rivers)
(Figs. 68–71)

Usingerina moapensis La Rivers 1950: 368–373.
Limnocoris moapensis: Sites and Willig 1994: 810.
USA: Nevada, Clark Co., Moapa
Length, 0.98 ± 0.01; width, 0.56 ± 0.01; n = 8; oviposited.

Overall appearance robust, elongate-oval (Fig. 68). Reticulation pattern generally consisting of pentagonal to heptagonal units, delimited by faintly impressed lines. Within each unit, chorion smooth, perforated by 15–60 aeropyles set in shallow individual sockets. Chorion smooth, devoid of papillae, tubercles, and protruberances other than micropyle. Anterior pole with micropyle set in concavity, immediately surrounded by modified chorion devoid of pattern and aeropyles. 2–3 distinct micropyles ($\bar{y}$ = 2.8, n = 10) arising from central point, extending outward in arcuate fashion (Figs. 69, 70).

Exochorion ca. ⅔ as thick as endochorion. Pore canals widest at base (Fig. 71).

Subfamily Naucorinae Stål 1876
Genus *Ilyocoris* Stål 1861
Ilyocoris cimicoides (Linnaeus)
(Figs. 72–77)

Nepa cimicoides Linnaeus 1758: 440.
Ilyocoris cimicoides: Stål 1861: 201.
Naucoris cimicoides: Rawat 1939: 123–127, Figs. 1–3.
CZECHOSLOVAKIA: southern Bohemia, Veselnad Lu Nic
Length, 2.25 ± 0.05; width, 0.56 ± 0.03; n = 8; dissected.

Overall appearance cylindrical and elongate with a 45 degree bend near middle (Fig. 72). Anterior pole flattened (Fig. 73), posterior pole rounded. Reticulation generally consisting of pentagonal to heptagonal units, delimited by faintly impressed boundaries (Fig. 74). Within each unit, chorion smooth, perforated by 50–90 aeropyles. Flattened anterior pole with elongate tumescences radiating outward from acentric micropylar plug (Fig. 75). Micropylar plug with four micropyles (Fig. 76), each of which is raised slightly above the remainder of the plug (Fig. 77).

Rawat (1939) described the egg as approximately 2 mm in length and cylindrical with an operculate, recurved end. Lebrun (1960) illustrated the position of the micropylar plug on the operculum (although not labeled as such) and Hinton (1981) reported the presence of three to four micropyles. This is the only naucorid documented to have endophytic oviposition (Rawat 1939, Cobben 1968).

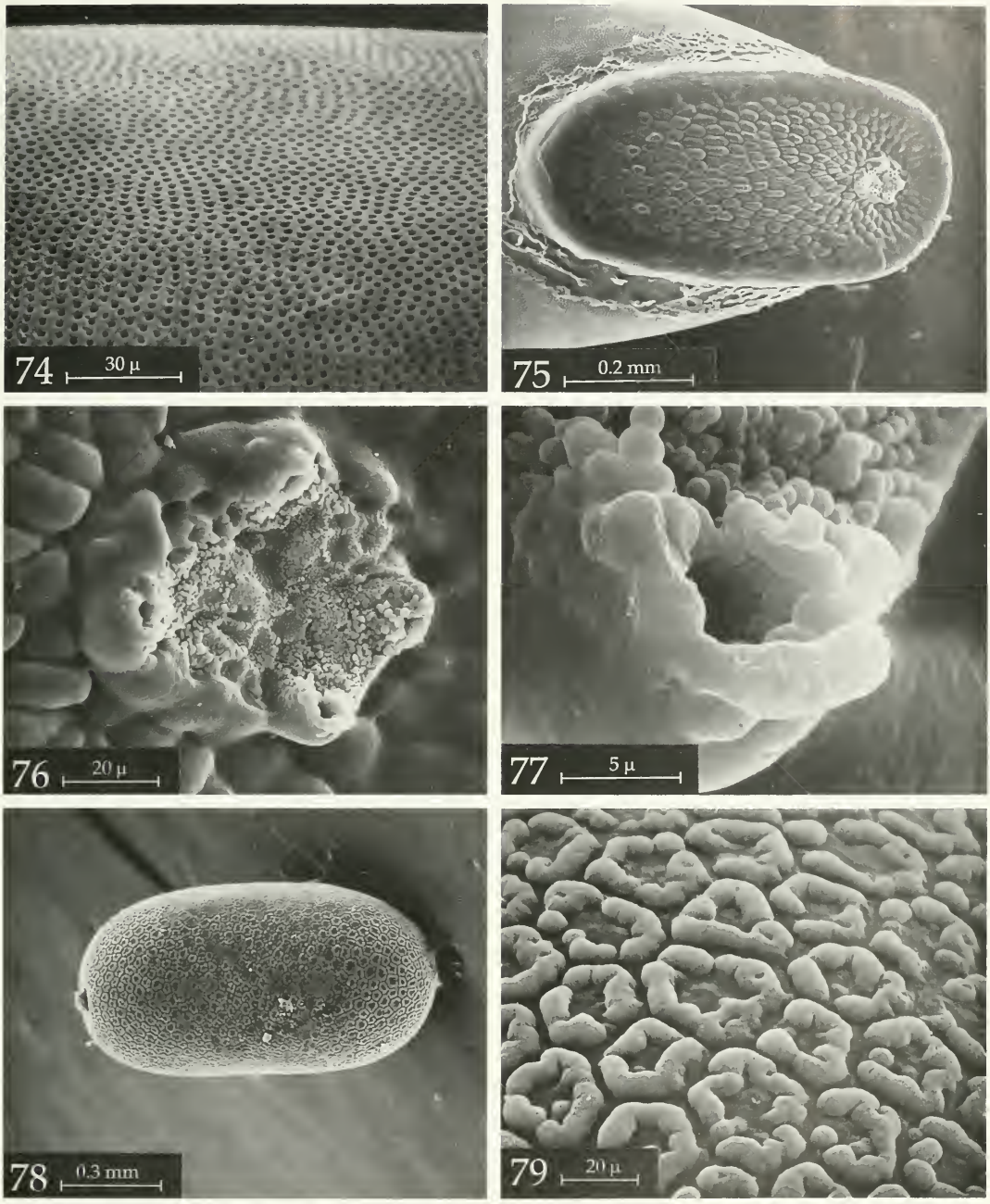
Genus *Pelocoris* Stål 1876
Pelocoris femoratus (Palisot de Beauvois)
(Figs. 78–81)

Naucoris femorata Palisot de Beauvois 1820: 237.
Pelocoris femoratus: Stål 1876: 144.
Pelocoris femorata: Torre Bueno 1903: 168–172.
Pelocoris carolinensis: Hungerford 1927: 80–82, Plate VI.
Pelocoris femoratus: McPherson et al. 1987: 291.
USA: Missouri, Boone Co., Columbia
Length, 1.17 ± 0.01; width, 0.64 ± 0.01; n = 10; oviposited.

Overall appearance elongate-oval (Fig. 78). Reticulation pattern generally consisting of pentagonal to heptagonal units. Within each unit, irregular and sometimes discontinuous elongate tumescence approximating boundary (Fig. 79). Anterior pole with micropylar plug set in shallow concavity. Micropylar plug somewhat amorphous and inconsistent in appearance, with micropyles opening laterally (Fig. 80). Number of micropyles indistinct, but apparently 2–3.

Exochorion ca. 3.5 × thicker than endochorion. Pore canals widest at middle and base (Fig. 81).

Using light microscopy, McPherson et

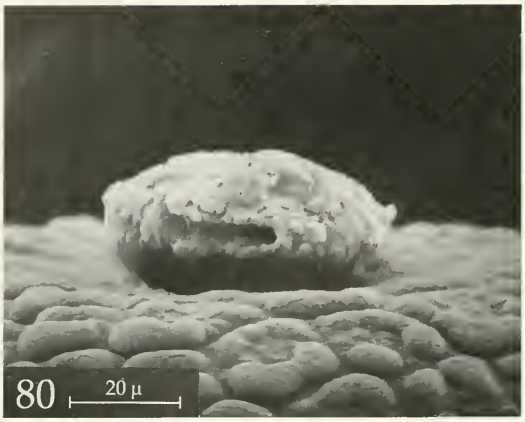


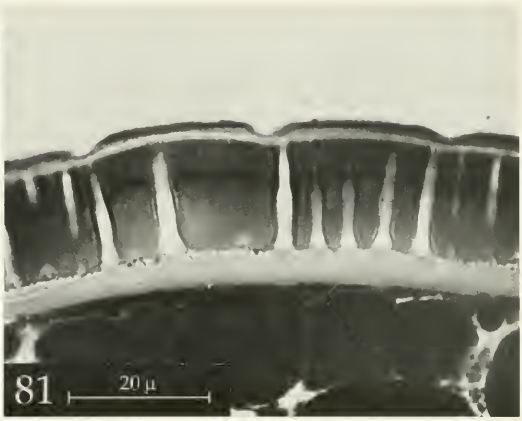
Figs. 74–79. 74–77, *Ilyocoris cimicoides*. 74, Chorion surface. 75, Anterior pole. 76, Micropylar plug. 77, Micropylar opening. 78, 79, *Pelocoris femoratus*. 78, Whole egg. 79, Chorion surface.

al. (1987) reported that the chorion has a primarily irregular hexagonal pattern and the micropylar plug is situated at the anterior end.

Discussion

Differences were evident in the chorion between incompletely developed and well-





Figs. 80–81. *Pelocoris femoratus.* 80, Micropylar plug. 81, Chorion section.

developed eggs. Eggs that were incompletely developed generally appeared to have a single point within each reticulation unit, which was raised and around which the chorion appeared to have flowed down onto the surface of the egg. This 'poured' appearance probably represented the site of chorion deposition for each follicular epithelial cell. Nonetheless, for dissected eggs, even though we selected eggs from the common oviduct or vagina for descriptions, the possibility exists that egg structure may have continued to develop prior to oviposition. For the 21 species of *Ambrysus* examined, chorionic sculpturing differs interspecifically and generally is species-specific. Although these differences were noted, other specific features were common among some of the species.

Previously, eggs were described and electron micrographs presented for *A. lunatus* (Sites and Nichols 1990), a member of the *signoreti* group. Other members of the *signoreti* group represented here are *A. inflatus, A. occidentalis,* and *A. portheo.* Generally, these four species share egg features including an acutely raised, fence-like reticulation forming a polygonal pattern, and minute papillae distributed generally over the surface. In addition, two species possess elongate, antheform processes. Eggs of other members of the *signoreti* group are likely to possess these features.

Eggs of the genus *Ambrysus* have been reported to have six micropyles (Hinton 1981), and those of an unspecified species from Aruba, Netherlands Antilles, usually have at least five (Cobben 1968). The individual micropylar tubes of *Ambrysus* are fused into a single, prominent plug (Cobben 1968). Our internal examinations have revealed two micropyles in each of three species of *Ambrysus* and three in two other species. Although it is likely that intraspecific variation exists in micropyle number for species of *Ambrysus,* as has been observed in species of other naucorid genera [e.g., *C. hungerfordi* (Sites and Nichols 1993)], we have observed only two and three micropyles. Thus, our data do not corroborate Hinton's (1981) report of six nor Cobben's (1968) report of five or more micropyles for species of *Ambrysus.*

In sharp contrast to *Ambrysus,* the number of micropyles for species of *Limnocoris* is clear with external examination because micropylar fusion is minimal. For *Limnocoris lutzi* and *Limnocoris* sp. [Ecuador, see Sites (1990)], two micropyles are clearly evident. Of 10 eggs of *Limnocoris moapensis* (La Rivers), eight had three micropyles whereas the other two had two micropyles. Previous reports for *Limnocoris* micropyles are nonexistent.

The number of micropyles for species of *Pelocoris* is unclear and the degree of fu-

sion differs interspecifically. Sites (1991) revealed two partially-fused micropyles for *P. poeyi*. Surprisingly, for *P. femoratus*, the micropyle number has not previously been given despite three separate descriptions of eggs [Torre Bueno 1903, Hungerford 1927 as *P. carolinensis* (see La Rivers 1948b), McPherson et al. 1987]. *Pelocoris femoratus* micropyles are fused into a plug ['micropylar boss' of Torre Bueno (1903)] similar to that of *Ambrysus*. The form of the plug is inconsistent, and a canal leading to a micropylar opening may be observed in some specimens.

In the only report for eggs of species of the subfamily Potamocorinae, which is considered by some to represent a distinct family level taxon (e.g., Štys and Jansson 1988), Cobben (1968) indicated that *C. kleerekoperi* has a single micropylar opening with several external mucous projections.

Systematic Value

The family Naucoridae is not blessed with even a modicum of somatic characters that varies among the higher taxa that may be used to elucidate systematic relationships. The principal characters that have been used for interspecific taxonomic distinctions have been adult male and female external genitalic features. Characters of nymphs and eggs have not been used, although López Ruf (1989) suggested that chorionic attributes may be valuable taxonomic characters externally at the species level and internally at the generic level. We concur with this assessment. Specifically, intergenerically variable characters include the relative widths of the chorionic inner and outer layers and pore canal configuration. Although the number of micropyles does not vary appreciably among these genera, the degree of external fusion of the individual micropylar tubes may be a taxonomically valuable character at generic or higher levels. External chorionic patterns are quite valuable as an interspecific diagnostic character in certain genera (e.g., *Ambrysus*). However, the pattern is invariant among the four species of *Limnocoris* that we have examined. Thus, the utility of this character in providing systematic resolution appears to be restricted to particular genera.

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NEW SPECIES OF HYDROPTILIDAE (TRICHOPTERA) FROM THE AMAZON REGION OF NORTHEASTERN PERU

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Abstract.—Two new species of *Neotrichia,* ***N. orejona*** and ***N. tirabuzona,*** five new species of *Oxyethira,* ***O. presilla, O. peruviana, O. vaina, O. picita,*** and ***O. hozosa,*** and one new species of *Orthotrichia,* ***O. shimigaya*** are described from the upper Amazon region in Peru.

Key Words: Microcaddisflies, Trichoptera, Hydroptilidae, Peru, Neotropics, new species

In 1992, Harris and Davenport described five new species of microcaddisflies from the Rio Sucusari and Rio Yanamono in the upper Amazon region of Peru (Fig. 1 in that paper). The collections were made in 1991 by Davenport during educational expeditions to the Explorama Lodge and the Explornapo Camp. Davenport made additional trips to the same region (as described in Harris and Davenport 1992) in January of 1993 and 1995. This paper reports on seven new species, two in the genus *Neotrichia,* one in the genus *Orthotrichia,* and four in the genus *Oxyethira,* from the most recent collections. An additional *Oxyethira* is described from an earlier collection in northern Peru.

Morphological terminology follows that of Marshall (1979). Length is measured from the top of the head to the wing tip and is given as a range with more than one specimen. Type material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), and in the collection of the senior author (SCH).

Neotrichia orejona Harris and Davenport, new species

(Fig. 1)

Diagnosis.—In many respects, this species is similar to *N. yanomonoa* Harris and Davenport, *N. cayada* Harris and *N. browni* Harris. All three share the elongate posterolateral extensions from the ninth abdominal segment and all have a hooklike phallic apex. The new species is readily separated by the triangular inferior appendages, the bifid subgenital plate and the serrated phallic processes.

Male.—Length 1.3 mm. Antenna with 18 segments. Brown in alcohol. Abdominal segment VIII annular. Segment IX in lateral view with narrow, elongate process from posterolateral margin; in ventral view with elongate, narrow lobes laterally, mesally with pair of thin, elongate processes each bearing small seta at apex. Segment X fused with IX, in dorsal view deeply incised mesally, pair of small setiferous lobes anteriorly. Inferior appendages triangular in lateral view, apex truncate bearing numerous setae; in ventral view rectanguloid, curving mesad. Subgenital plate beaklike in lateral view with narrow seta-bearing process dorsally; wide basally in ventral aspect with bifid processes, narrowing posteriorly. Phallus tubular, apex divided into two flattened serrate processes, ejaculatory duct protruding subapically, thin paramere encircling shelf near midlength.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Lor-

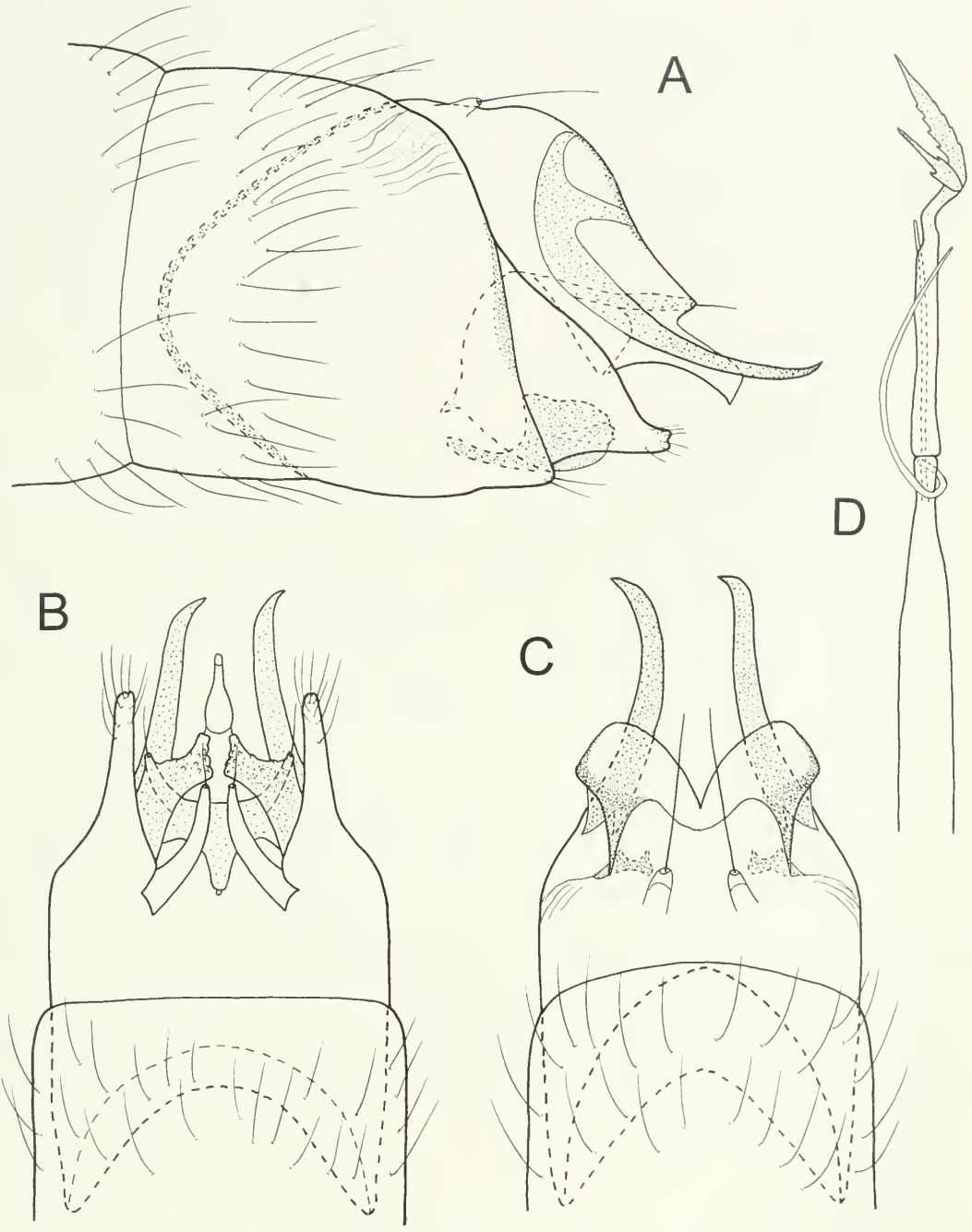

Fig. 1. *Neotrichia orejona*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

eto, edge of Rio Sucusari backwater, adjoining Explornapo Camp, 16 January 1993, L. J. Davenport (NMNH).

Etymology.—Named for the Orejone indians which live in the area.

***Neotrichia tirabuzona* Harris and Davenport, new species**

(Fig. 2)

Diagnosis.—This new species falls within the *caxima* group, as established by Mar-

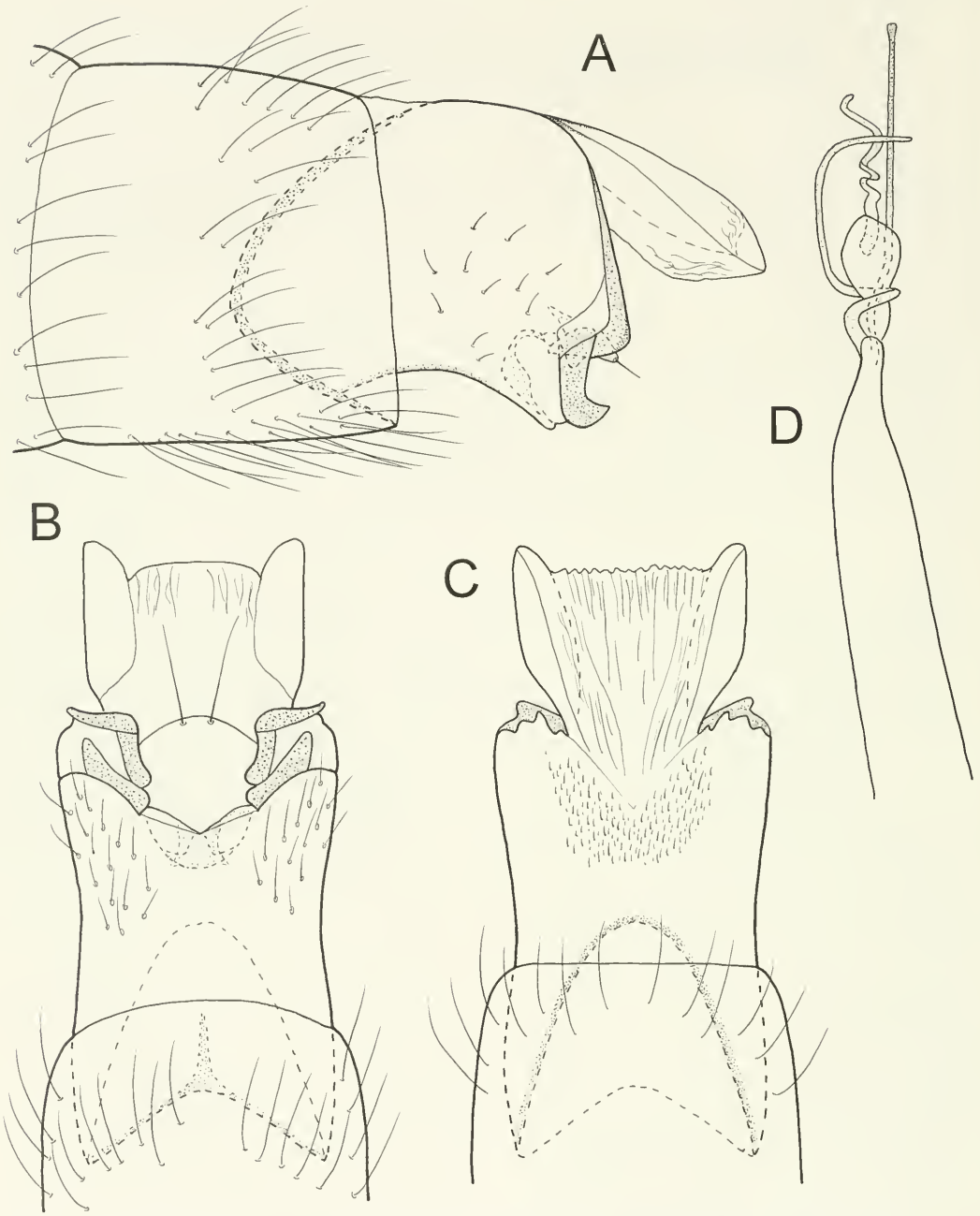

Fig. 2. *Neotrichia tirabuzona*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

shall (1979), with greatest similarity to *N. rotundata* Flint and *N. dientera* Harris. The hooklike inferior appendages and spiral process from the phallus apex are characteristic for *N. tirabuzona*.

Male.—Length 1.5–1.7 mm. Antenna with 18 segments. Brown in alcohol. Abdominal segment VIII annular. Segment IX in lateral view square, curving ventrally to posteroventral projection; in ventral view square, emarginate on posterior and anterior margins. Segment X lobate in lateral view;

in dorsal view partially fused with IX at narrow base, widening distally with truncate incision apically. Inferior appendages hook-shaped in lateral view; in ventral view square and widely separated, sclerotized bands basally, posteriorly, and mesally. Subgenital plate a narrow shelf in lateral view; in ventral view rounded distally, pair of elongate setae mesally. Phallus wide at base and at rounded apex, spiral process apically, ejaculatory duct thin and elongate, protruding apically, elongate paramere encircling shaft beyond midlength.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, edge of Rio Sucusari backwater, adjoining Explornapo Camp, 16 January 1993, L. J. Davenport (NMNH). Paratypes, Peru, same data as holotype, 7 ♂ (NMNH, SCH).

Etymology.—Spanish, corkscrew, referring to the spiral process from the phallus apex.

Orthotrichia shimigaya Harris and Davenport, new species
(Fig. 3)

Diagnosis.—The genus *Orthotrichia* is represented by six species in the Nearctic region, with two, *O. aegerfasciella* (Chambers) and *O. cristata* (Morton), extending into the Neotropical region. *Orthotrichia shimigaya* is the first species of the genus to be reported exclusively from South America. The species is easily recognized by the structure of the inferior appendages.

Male.—Length 2.5–2.6 mm. Antenna with 32 segments. Brown in alcohol. Abdominal segment VII with elongate posteromesal process from venter. Segment VIII annular. Segment IX reduced ventrally to narrow bridge, a rounded lobe posteroventrally; in dorsal view incised posterolaterally, mesally a truncate lobe. Segment X in lateral view divided into pair of thin, elongate processes, turned laterad at apex; in ventral view, narrowly incised on posterolateral margin, left lobe wider and more truncate than right. Inferior appendages in lateral view short and triangular; in ventral view asymmetrical, left appendage with pair of thin, seta-bearing processes from posterolateral margin, right appendage narrowing mesad and curving downward, single seta-bearing process from posterolateral margin. Subgenital plate in lateral view a narrow shelf; in ventral view tonguelike, pair of setae from rounded, posterior margin. Phallus tubular, apical half with ringlike crenulations, tipped with pair of narrow lateral lobes, paramere encircling shaft at midlength.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, small stream just outside grounds of Explorama Inn, 20 January 1995, L. J. Davenport (NMNH). Paratype. Peru, Loreto, backwater creek at outlet of Lake Shimigay, ca. 2 km. upstream Rio Napo from mouth of Rio Sucusari, 15 January 1993, L. J. Davenport, 1 ♂ (NMNH).

Etymology.—Named for Lake Shimigay, one of the type localities for the species.

Oxyethira presilla Harris and Davenport, new species
(Fig. 4)

Diagnosis.—This new species is most similar to *O. rareza* Holzenthal and Harris, with which it shares the asymmetrical genitalic features. The multiple processes at the apex of the phallus and the long looping processes from the venter of segment IX will readily identify *O. presilla.*

Male.—Length 2.2 mm. Antenna with 38 segments. Brown in alcohol. Abdominal segment VII annular, lacking posteromesal process from the venter. Segment VIII tapering posteriorly, deeply incised on posterior margin in ventral and dorsal views. Segment IX complex, elongate anteriorly and tapering posteriorly with several asymmetrical processes, ventrally divided into two processes, lowermost upturned at midlength and slightly widening, uppermost process thin, posteriorly curving into a loop; dorsal process narrow anteriorly, widening to transverse plate at midlength; in

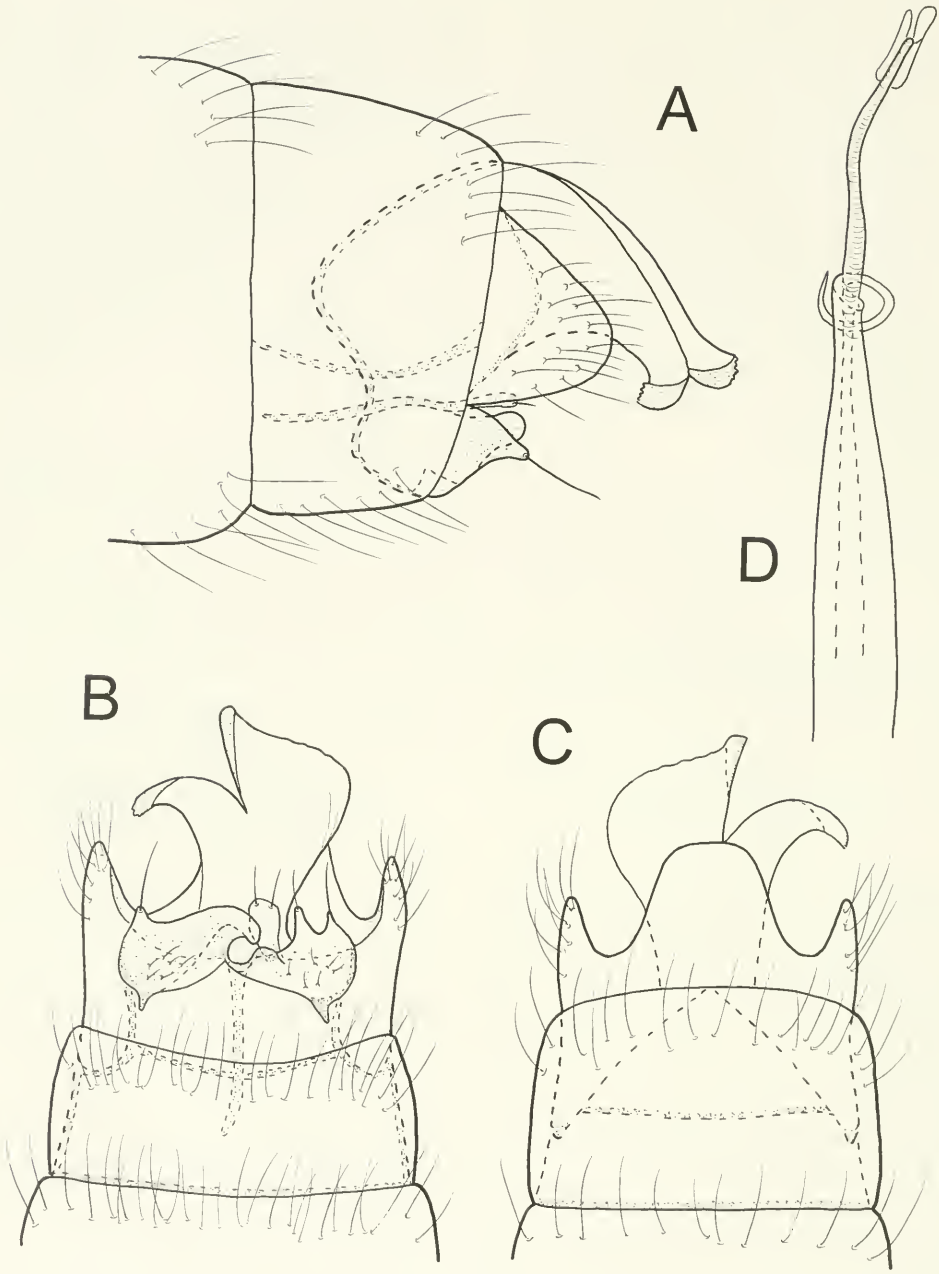

Fig. 3. *Orthotrichia shimigaya*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

ventral view deeply incised, right lateral margin with two processes, apical process narrow, subapical process wider and projecting more mesad, left lateral margin divided into two elongate thin processes. Tergum X apparently fused with IX as apex of rectangular plate on IX. Inferior appendages and subgenital plate not evident. Phallus wide at base, narrowing at midlength, apical portion widening with several scler-

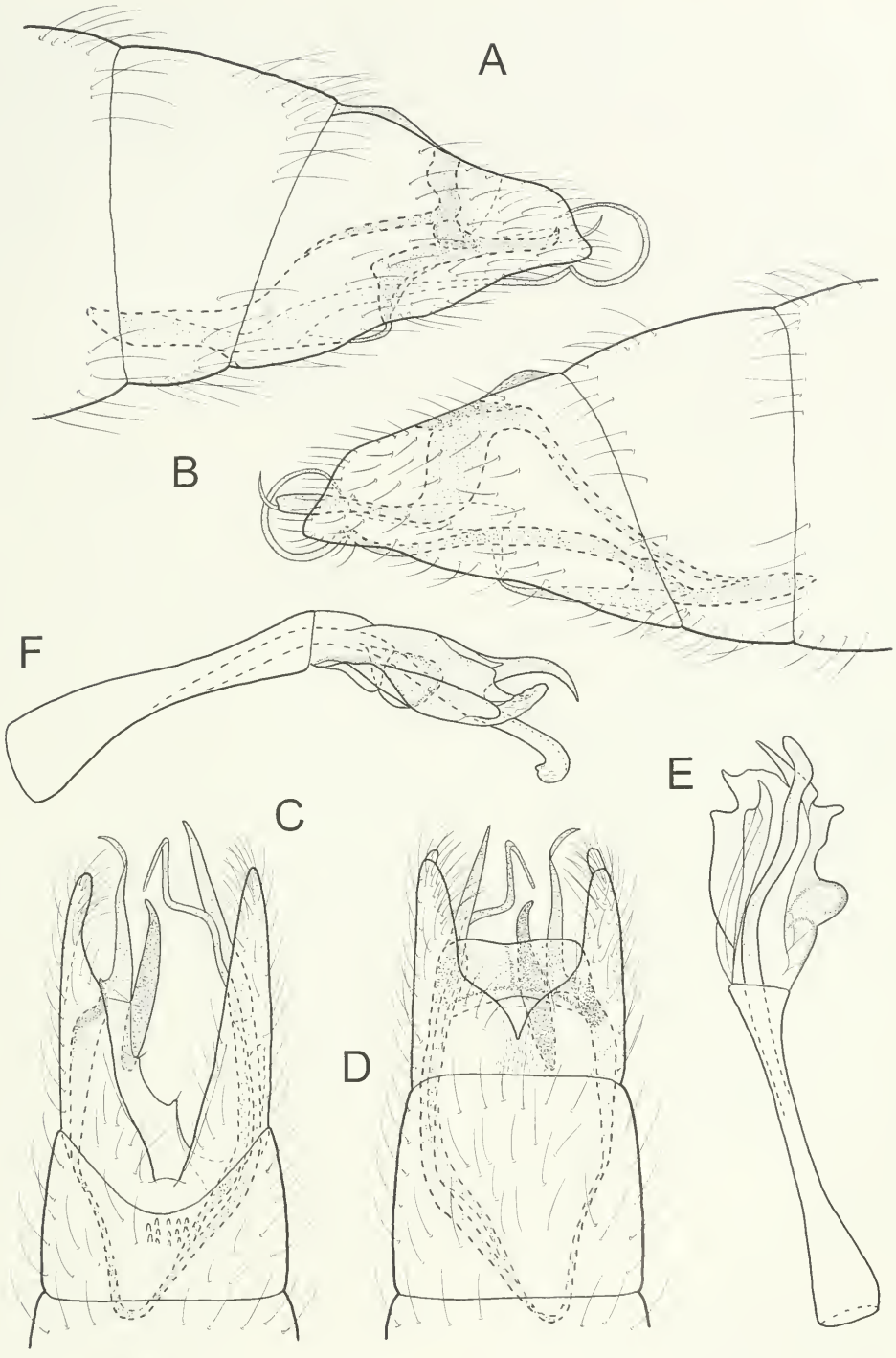

Fig. 4. *Oxyethira presilla,* male genitalia. A, Lateral, left side. B, Lateral, right side. C, Ventral. D, Dorsal. E, Phallus, dorsal. F, Phallus, lateral.

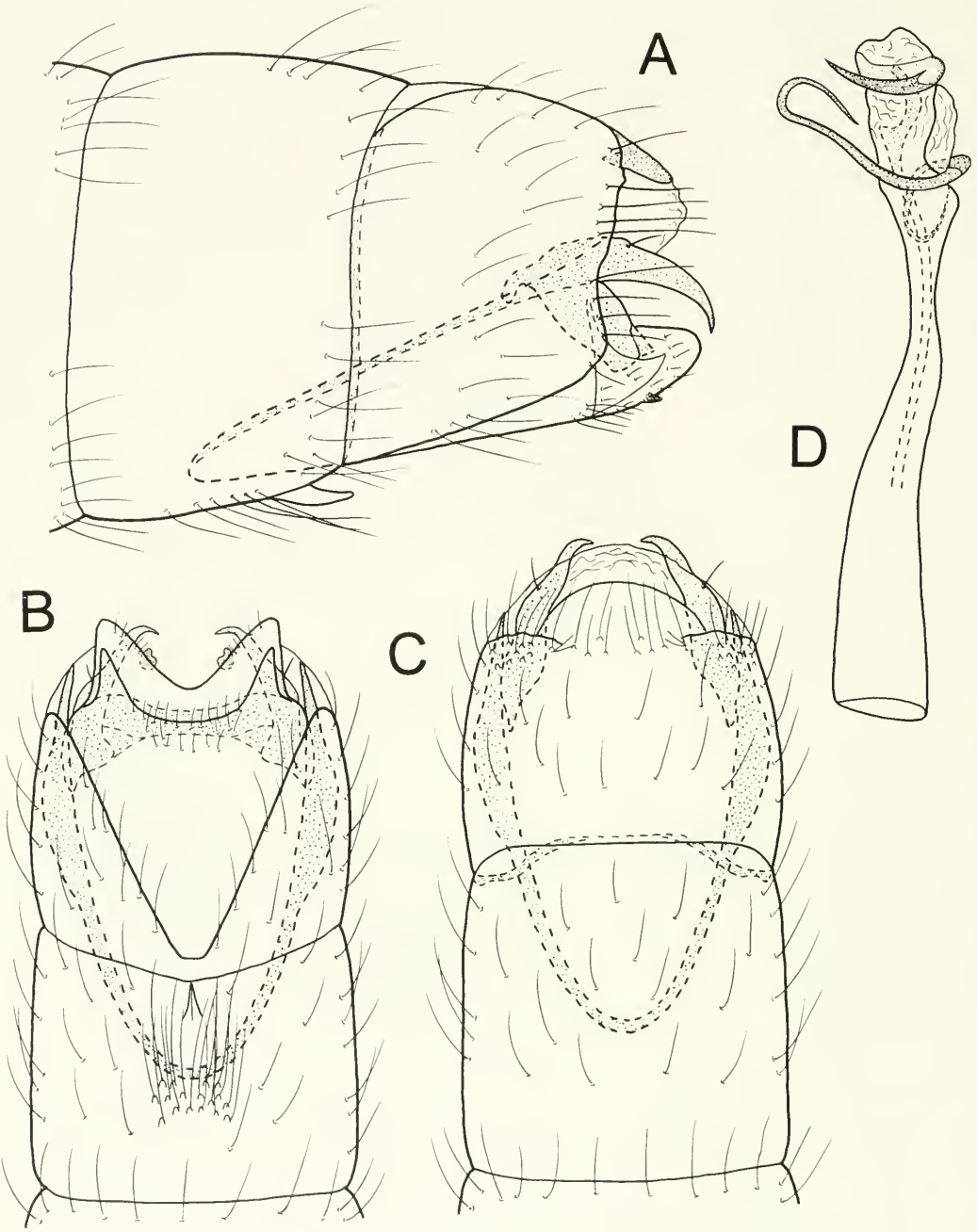

Fig. 5. *Oxyethira peruviana*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

otized processes on lateral margins, ejaculatory duct protruding distally as sclerotized, sinuate process.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, Yanamono Creek at jungle's edge, near Explorama Lodge, 12 January 1995, L. J. Davenport (NMNH).

Etymology.—Spanish, loop, refering to the distinctive process from segment IX.

Oxyethira peruviana Harris and Davenport, new species
(Fig. 5)

Diagnosis.—This species appears to be most similar to *O. spissa* Kelley, a member of the *pallida* group of Kelley (1984). Both species have a prominent posterolateral process from segment IX and inconspicuous subgenital plate, but *O. peruviana* differs in the elongate processes from the phallus apex and the longer inferior appendages.

Male.—Length 2.3 mm. Antenna with 29 segments. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from the venter. Segment VIII annular in lateral view; deeply incised posteriorly in ventral view; rounded posteriorly in dorsal view. Segment IX triangular in lateral view, greatly reduced dorsally, acute, downturned curved process posterolaterally, posteroventrally with short, triangular process; in ventral view, posterior margins with three processes, lateralmost thin and acute, ventromesal processes triangular, dorsomesal processes tapering and angled inward. Segment X a short, membranous lobe; in dorsal view wide and rounded posteriorly. Inferior appendages short and rounded in lateral view, short spine from venter; in ventral view fused mesally, triangular laterally with small bilobed sclerite from mesal margins. Subgenital plate rectanguloid and slanted posteroventrally in lateral view; in ventral view a narrow, transverse band; lacking bilobed process. Phallus tubular, widening at apex which bears an elongate paramere subapically and short, transverse process at apex; ejaculatory duct bifid at apex.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, tributary to Rio Yanamono at Explorama Lodge, 11 March 1991, L. J. Davenport (NMNH).

Etymology.—Named for the country of Peru.

Oxyethira vaina Harris and Davenport, new species
(Fig. 6)

Diagnosis.—This new species is most similar to *O. orellanai* Harris and Davenport, a member of the *Tanytrichia* subgenus of Kelley (1984), which was also collected at the same locality on the Rio Sucusari. The new species is separated by the shorter anteroventral extension of segment IX and the triangular inferior appendages, which in ventral view are fused mesally.

Male.—Length 2.3 mm. Antenna with 28 segments. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from the venter. Segment VIII tapering posteroventrally in lateral view; in ventral view deeply incised mesally on posterior margin; posterior margin of dorsum with mesal truncate incision. Segment IX reduced posterodorsally to narrow bridge, narrowing and extending anteriorly through segment VII. Tergum X lobate, membranous. Inferior appendages short and triangular in lateral view; fused in ventral view, round mesal incision creating thin triangles laterally, stout seta from apex, dorsal lobes along mesal margins. Subgenital plate in lateral view a narrow shelf with bilobed process curving over it posteriorly; in ventral view a narrow rectangle with thin lateral arms angled mesad, bilobed processes widely separated with setae at tips. Phallus tubular with lateral sheath, narrow sclerite running contiguous with ejaculatory duct.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, edge of Rio Sucusari backwater, adjoining Explornapo Camp, 16 January 1993, L. J. Davenport (NMNH).

Etymology.—Spanish, sheath, referring to the lateral ribbonlike band of the phallus.

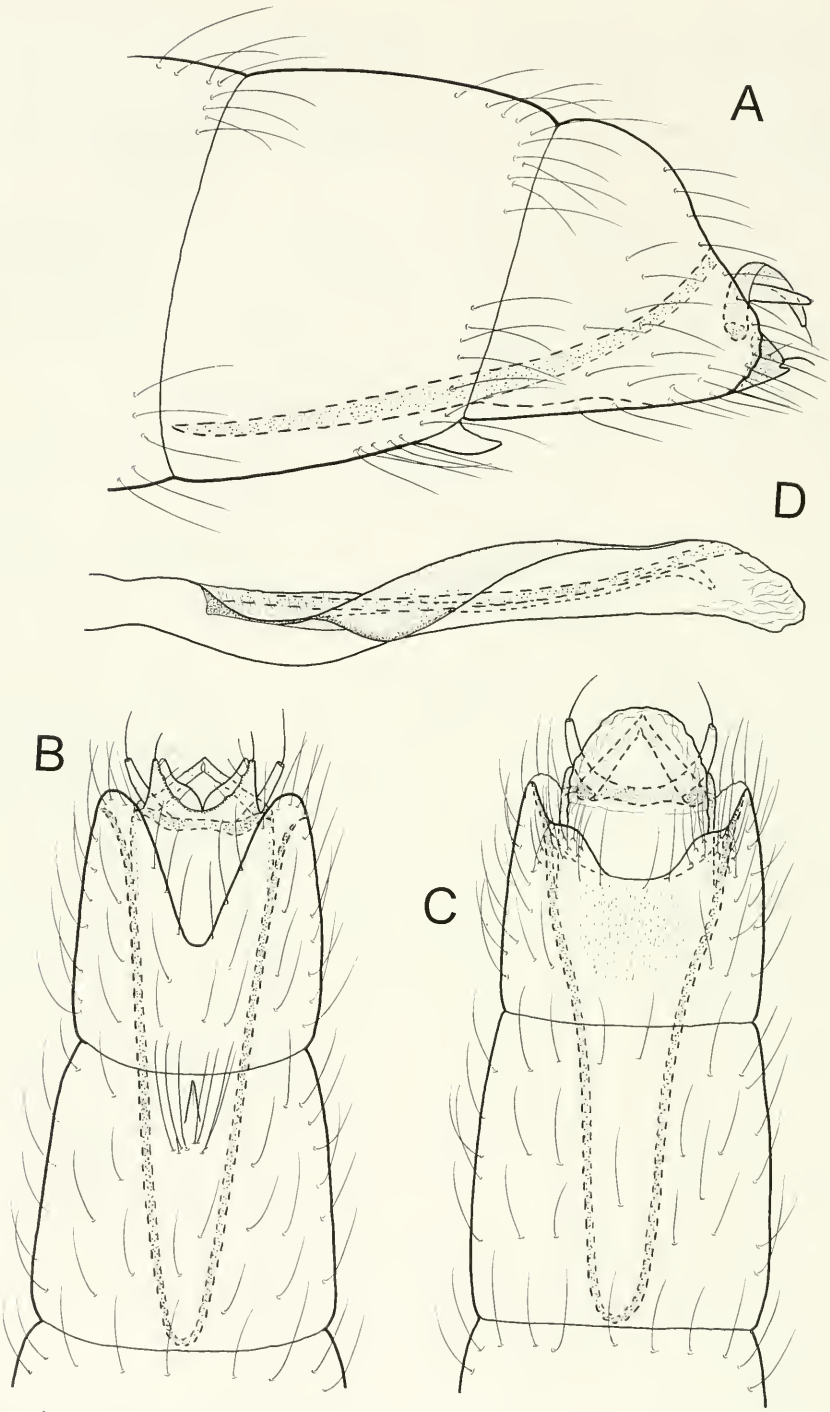

Fig. 6. *Oxyethira vaina,* male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral.

Oxyethira picita Harris and Davenport, new species
(Fig. 7)

Diagnosis.—Although this species appears to be a member of the *Tanytrichia* subgenus of Kelley (1984), there is some resemblance to *O. zilaba* (Mosely) of the subgenus *Loxotrichia*. The new species is distinguished by the elongate subgenital plate and the pair of small lateral spines on the tenth tergite.

Male.—Length 2.3 mm. Antenna with 26 segments. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from the venter. Segment VIII tapering posteroventrally to rounded apex, short process dorsolaterally; in ventral view deeply incised posteriorly; in dorsal view also deeply incised with three acute processes mesally. Segment IX extending anteriorly into segment VI, posteriorly short and reduced dorsally to thin process. Segment X lobate in lateral view; in dorsal view rectanguloid with rounded apex, pair of short spines posterolaterally. Inferior appendages in lateral view elongate and tapering posteriorly, apex with ventral spine and dorsal seta-bearing process; in ventral view fused posteriorly, apex with lateral seta-bearing processes and median truncate process, heavy seta between processes, lateral margins gently emarginate. Subgenital plate curving anteroventrally, posteriorly elongate and narrowing to acute apex, transverse bilobed process thin and elongate; in dorsal and ventral views divided at base into two elongate processes which narrow and cross apically, bilobed process thin, diverging distally. Phallus tubular, small lateral spines below midlength, widening apically, pair of lateral processes which are curved distally, ejaculatory duct between the two processes.

Female.—Unknown.

Type material.—Holotype, ♂. Peru, Loreto, edge of Rio Sucusari backwater, adjoining Explornapo Camp, 16 January 1993, L. J. Davenport (NMNH).

Etymology.—Spanish, small sharp point, referring to the small spines of the tenth tergite.

Oxyethira hozosa Harris and Davenport, new species
(Fig. 8)

Diagnosis.—This species is closely related to *O. scaeodactyla* Kelley, particularly in the structure of the phallus and the inferior appendages. The new species differs in the acute, distal point of the subgenital plate, the short bilobed process, and the more complete ninth segment.

Male.—Length 2.4 mm. Both antenna broken. Brown in alcohol. Abdominal segment VII annular with short, posteromesal process from the venter. Segment VIII rounded posteriorly in lateral view; in ventral view, deep mesal incision; emarginate dorsally. Segment IX tapering anteriorly, a narrow band posterodorsally, narrow process posteroventrally; ventrally with lateral margins produced into sharp points which extend beyond VIII, pair of fingerlike processes mesally; dorsally fused posteriorly with X. Segment X a short membranous lobe in lateral view; dorsally square in shape with posterior margin truncate. Inferior appendages short and truncate; in ventral view, incised mesally and fused, narrowing posterolaterally and bearing stout seta. Subgenital plate in lateral view strongly curving ventrad, apex with acute apical point; in ventral view wide with lateral edges rounded, mesally with knoblike process; bilobed processes short in lateral view; in ventral view widely separated and sinuate. Phallus short, distally narrowing to conspicuous hook, ejaculatory duct sinuate and enclosed within membranous lobe.

Female.—-Unknown.

Type material.—Holotype, ♂. Peru, Loreto, Rio Yanamono just below Explorama Lodge, 10 January 1993, L. J. Davenport (NMNH).

Etymology.—Spanish, sicklelike, referring to the distinctive phallus.

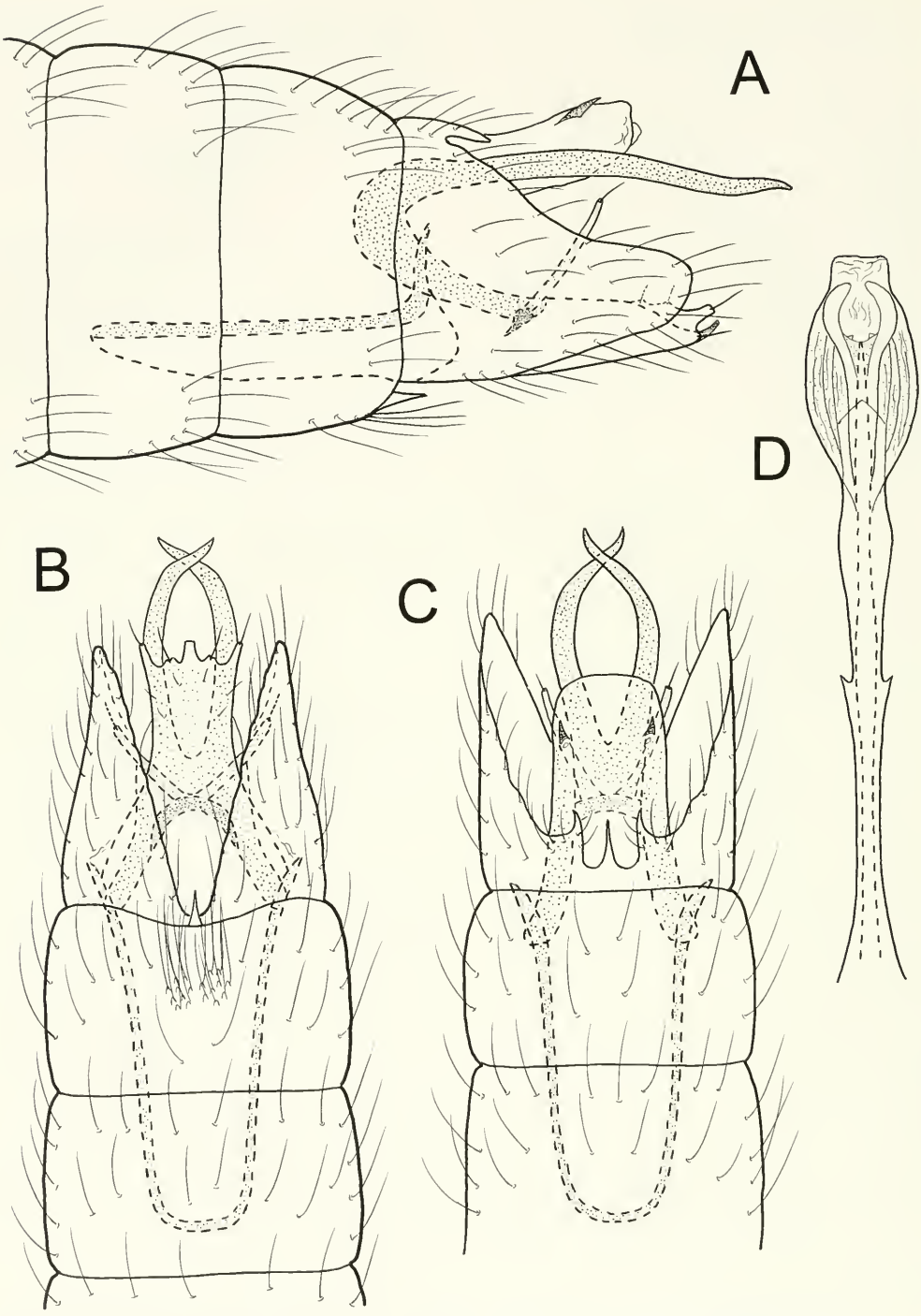

Fig. 7. *Oxyethira picita*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

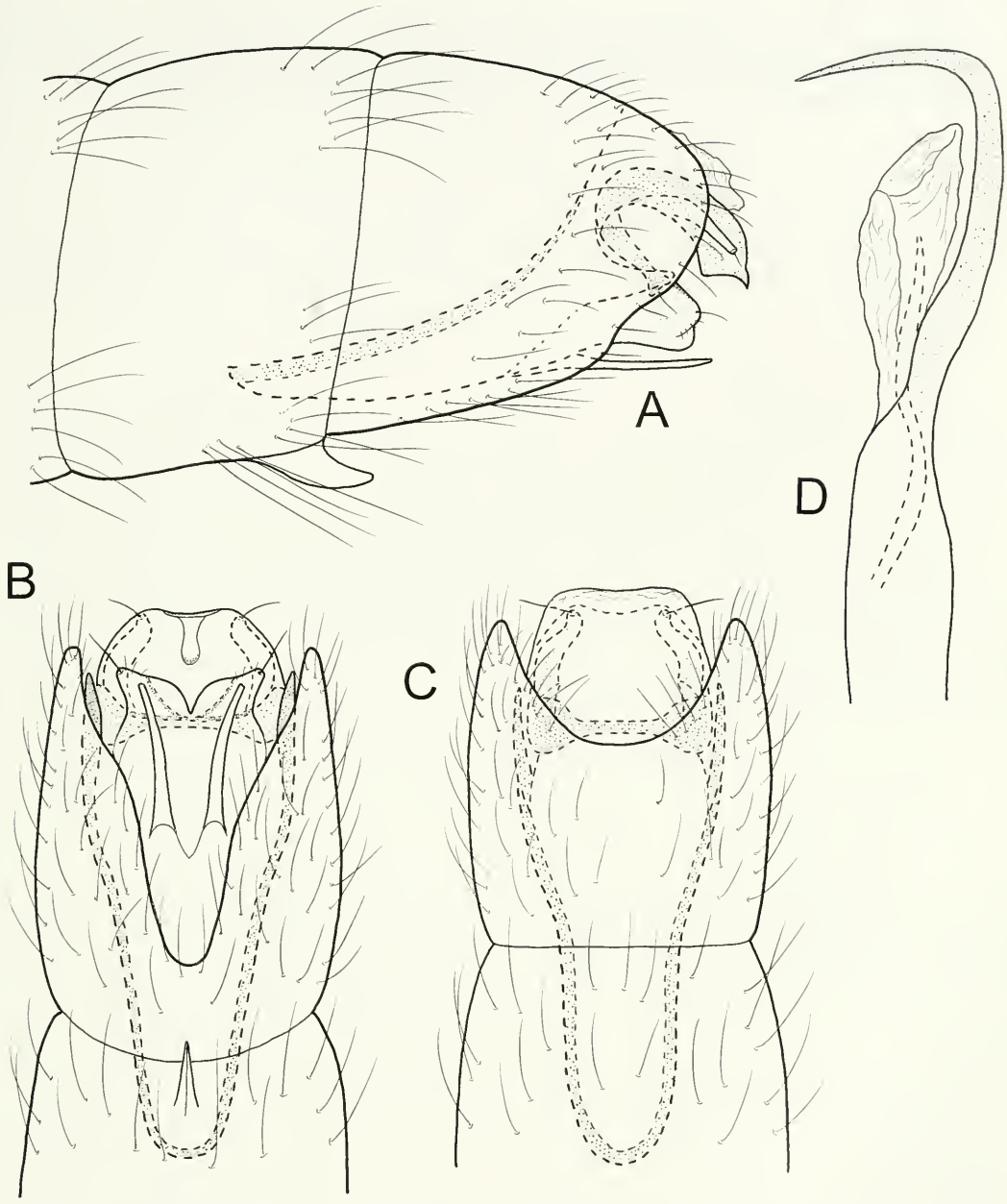

Fig. 8. *Oxyethira hozosa*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, dorsal.

Acknowledgments

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AN EXAMINATION OF THE NORTH AMERICAN APHID SPECIES CURRENTLY PLACED IN *OVATUS* VAN DER GOOT (HEMIPTERA: APHIDIDAE) WITH THE DESCRIPTION OF A NEW GENUS

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Abstract.—The current placement in *Ovatus* of four endemic North American aphid species is critically examined. Results of cladistic analyses clearly indicate that these four species are not congeneric with Palearctic *Ovatus* and that they are more closely related to *Myzus* Passerini. Cladistic evidence is provided to justify the erection of a new genus, ***Abstrusomyzus* n. gen.,** for the four endemic North American species formerly placed in *Ovatus*. This resulted in four new combinations: *Abstrusomyzus leucocrini* (Gillette & Palmer) **n. comb.**, *Abstrusomyzus phloxae* (Sampson) **n. comb.**, *Abstrusomyzus reticulatus* (Heie) **n. comb.**, and *Abstrusomyzus valuliae* (Robinson) **n. comb.** Information on each of the four species is compiled and presented. Illustrations are provided, along with a key to the species of the new genus and notes on the single remaining species of *Ovatus* in North America, *Ovatus crataegarius* (Walker).

Key Words: polyphagy, *Myzus, Ovatus,* new genus, cladistics

Most aphids are extremely host specific, feeding on one or a few species of plants that are usually closely related (Eastop 1973). Many of the most pestiferous aphids known differ dramatically from this normal pattern by being polyphagous on plants in widely divergent families. Well-known polyphagous pests include the green peach aphid [*Myzus persicae* (Sulzer)], the potato aphid [*Macrosiphum euphorbiae* (Thomas)], and the cotton aphid (*Aphis gossypii* Glover). These aphids can cause serious problems even when they feed on a crop in low numbers, since they can transmit plant viruses between their phylogenetically disparate host plants. Very few polyphagous aphids are not pests. Given the fact that many of the most serious pest aphids are polyphagous, it is important to study newly-discovered cases of polyphagy in aphids. As polyphagous aphids are likely to some day become pests, prior knowledge of their biology, taxonomy, and evolution will facilitate an effective reaction to their emergence as pests.

Ovatus phloxae (Sampson) is one of the few polyphagous aphids that so far is not a pest. It was described in 1939 from *Phlox subulata* from Berkeley, California. Since then it has been found on eighteen plants in fourteen families (Table 1). It has been collected in most regions of the United States and probably occurs in most temperate parts of North America. Most plants on which this aphid has been found have a basal rosette of leaves, or tend to be prostrate. The aphid usually lives in the crown or on the lower leaves. It is possible that this species is more habitat specific than host specific, much as in *Rhopalosiphum nymphaeae* (L.), which

Table 1. Host plants and distributions for five species heretofore placed in *Ovatus*.

Aphid Species	Host Plants	Distribution
Ovatus crataegarius (Walker)	Rosaceae	Almost
	Crataegus spp.	worldwide,
	Cydonia spp.	with a
	Malus spp.	Palearctic
	Lamiaceae	origin
	Mentha spp.	
	some other Lamiaceae	
Ovatus leucocrini (Gillette & Palmer)	Liliaceae	Colorado
	Leucocrinum montanum	
Ovatus phloxae (Sampson)	Apocynaceae	Canada:
	Apocynum androsaefolium	British
	Apocynum sp.	Columbia
	Asteraceae	
	Achillea sp.	U.S.A.:
	Agoseris sp.	California
	Centaurea sp.	Colorado
	Brassicaceae	Maryland
	Capsella bursa-pastoris	Mississippi
	Caryophyllaceae	Nebraska
	Cerastium vulgatum	Oregon
	Stellaria crispa	Pennsylvania
	Cyperaceae	Utah
	Carex densa	Virginia
	Fabaceae	
	Trifolium sp	
	Hydrophyllaceae	
	Phacelia nemoralis	
	Liliaceae	
	"Lilies"	
	Plantaginaceae	
	Plantago major	
	Polygonaceae	
	Polygonum paronychia	
	Ranunculaceae	
	Ranunculus sp.	
	Polemoniaceae	
	Phlox subulata	
	Rubiaceae	
	Galium sp.	
	Violaceae	
	Viola sp.	
Ovatus reticulatus Heie	Oxalidaceae	North Carolina
	Oxalis ?stricta	
Ovatus valuliae (Robinson)	Rosaceae	Manitoba
	Fragaria vesca	

feeds widely on aquatic and semiaquatic plants. If this were true, *O. phloxae* could emerge at any time as a pest of a crop with an appropriate growth habit. Therefore a study of North American *Ovatus* was undertaken to provide needed information regarding *O. phloxae* and three closely related endemic North American aphids currently placed in *Ovatus*. The relationship of these four species to Palearctic *Ovatus* is examined using cladistics, and a new genus is proposed for them based on these analyses.

Materials and Methods

Most specimens studied are housed in the National Collection of Aphidoidea (USNM, located at the Systematic Entomology Laboratory, USDA, Beltsville, Maryland, USA). Others were obtained on loan from The Natural History Museum, London (BMNH); Agriculture Canada, Vancouver, British Columbia (UBC); University of California, Berkeley (UCB); and Oregon State University, Corvallis (OSU).

Aphids were mounted on microscope slides in Canada balsam or Hoyer's medium, and observed under phase contrast microscopy. Terminology follows Miyazaki (1987). Drawings were made by the first author using a camera lucida.

Cladistic analyses were performed using PAUP 3.1.1 (Swofford 1993) and MacClade 3.01 (Maddison and Maddison 1992) on 23 taxa using 25 characters. Apterous and alate viviparae were included in the character analysis, supplemented by one character of the first instar nymph. All characters were treated as unordered.

Ovatus van der Goot

Ovatus has most recently (Remaudière and Remaudière 1997) been used for fourteen *Myzus*-like aphids, which generally migrate between Pomoidea and various Lamiaceae, or are monoeceous on either of these groups. Nine of the fourteen species fit this pattern of host plant association. One exception is the single member of the subgenus *Ovatoides, Ovatus (Ovatoides) inulae* (Walker). This species feeds on Asteraceae and differs morphologically from most *Ovatus* by the nearly complete lack of spinulation on the head and first two antennal segments, and the long, setose ultimate rostral segment. The other four species that do not conform with the Pomoidea/Lamiaceae host plant association are the four endemic North American species [Table 1, excluding *Ovatus crataegarius* (Walker)]. These species feed on herbs from a diverse set of plant families, and none of them is known from Pomoidea or Lamiaceae. Morphologically these species differ from most Palearctic *Ovatus* by the dark bars and blotches on the abdominal tergum of the alate vivipara (Figs. 17, 18), first tarsal chaetotaxy of 3,3,2, and the peculiarly shaped siphunculus (Figs. 9–12).

The first to place one of these species in *Ovatus* was Hille Ris Lambers (1966), who transferred *Phorodon phloxae* to *Ovatus* without any explanation. Heie (1972) described *Ovatus reticulatus*, and Eastop and Hille Ris Lambers (1976) transferred *Myzus leucocrini* Gillette and Palmer and *Myzus valuliae* Robinson without explanation. The obviously close relationship among these four species dictated that they be placed together in the same genus, but their morphological and biological differences from Palearctic *Ovatus* causes doubt about their current generic placement.

Cladistic Analyses

This study attempts to determine whether the four North American species currently placed in *Ovatus* will cluster together, and whether they will form their own group, form a part of *Ovatus*, or fall within another genus. Doing this requires that the cladistic analysis include several species from one or more genera to which the species in question might be more closely related than they are to *Ovatus*. These cladistic analyses are meant to explore the proper generic placement of the four endemic North American species currently placed in *Ovatus* and are not meant to resolve species-level issues for the other aphids included in the analysis.

Choice of appropriate comparative groups for a test of the proper placement of the four endemic North American species is particularly troublesome in the case of *Ovatus* for at least three reasons. First, the fact that the analysis deals with aphids presents problems in itself (see Jensen 1997 for some discussion of this issue). Aphids are highly progenetic *sensu* Gould (1977), and because of their conservative morphology most genera lack apomorphic characters. Instead, there is

essentially a large pool of characters that occur across a wide range of aphid taxa, and many genera are recognized on the basis of a unique combination of these characters. Aphid genera are also frequently defined by the absence of one or more characters typical in genera to which they are most similar morphologically. These facts, in combination with the lack of work on the evolution of the commonly used aphid characters, make deductions about relatedness difficult.

The second problem that *Ovatus* poses is biogeographical. As currently understood, the genus is Holarctic, with ten species native to Eurasia, and four native to North America. Perhaps, then, comparative species should be drawn from related genera on both continents. Nearly all species of Myzina, the subtribe to which *Ovatus* belongs, are endemic to Eurasia, with the subtribe's greatest diversity in southern and eastern Asia. Therefore, choosing Eurasian species for comparison is easy. But examination of the native aphid fauna of North America shows that there are only a handful of Myzina native to this continent. These native species are mostly specialized moss and sedge feeders such as *Myzodium* Börner and *Carolinaia* Wilson. There are few other native North American Myzina besides the four putative *Ovatus,* and several species of *Hyalomyzus.* In other work (Stoetzel, Miller and Jensen, in preparation), evidence has been found for the monophyly of *Hyalomyzus* Richards of North America. This leaves few North American groups to which the four *Ovatus* could belong.

Thirdly, the four North American species currently placed in *Ovatus* are extremely similar and possess some unique characteristics. For example, they all have siphunculi more or less cylindrical, but slightly expanded apically (Figs. 9–12). Two of the species also tend to have more than three pairs of setae on the cauda, whereas most Myzina have two or three pairs. The four North American species also have a distinctive pattern of pentagonal or hexagonal reticulation on their terga in the apterous viviparous female. These peculiarities make them isolated morphologically from most of the Myzina and make the choice of appropriate species for the current analysis more difficult.

Myzus has for a long time been used for a great diversity of species of Myzina. This can be illustrated by examining the list of Eastop and Hille Ris Lambers (1976). They list 53 valid species of *Myzus,* and 40 others that were described in *Myzus,* but subsequently transferred to 27 other genera. The range of species included in the genus has varied from one author to another during this century. In North America most workers have dealt with the genus in a broad sense (Mason 1940, Palmer 1952). Mason states that *Myzus* can be recognized among the Macrosiphina in his tribe Aphidini by the convergent frontal tubercles. Thus in his revision of the genus, Mason (1940) included 20 species that are today scattered among six genera. Despite all this modification or restriction of the definition of the genus, *Myzus* still contains a wide array of species and is quite likely polyphyletic. The diversity of species in *Myzus* and the lack of another genus that is clearly related to the four species in question indicate that *Myzus* is the best choice for use in this analysis. *Myzus* provides a wide array of species to which the four endemic North American species might prove to be closely related.

Species Included in the Analyses

Included in the analysis were *Ovatus phloxae* and three very similar North American species, *O. leucocrini, O. reticulatus,* and *O. valuliae.* For purposes of testing their relationship to Palearctic *Ovatus,* six other *Ovatus* species were studied, including *Ovatus (Ovatoides) inulae,* the only member of its subgenus. These were chosen based on their availability in the collection of the USNM and material obtained on loan. Thus ten of the world's fourteen *Ovatus* species were analyzed. Adequate material of the other Eurasian species currently placed in *Ovatus* was not available.

Ten species of *Myzus* were included,

Table 2. Data matrix used in the cladistic analyses. Question marks indicate missing data, † indicates a 0/1 polymorphism, and a ‡ indicates a 0/2 polymorphism.

	111111111 122222 2 123456789012345678 901234 5
H. eriobotryae	000000000000001110 111011 0
H. jussiaeae	000000000100001110 110011 ?
H. mitchellensis	000111010000101110 111011 0
M. ascalonicus	†201†0101010101110 †††000 1
M. cerasi	000000000000000000 000000 0
M. certus	0001100‡1010101010 000100 1
M. cymbalariae	120100001110001110 010000 1
M. dycei	0000†0001110100110 010110 1
M. hemerocallis	0201100‡1000100010 000011 0
M. lythri	000010000000100010 000000 0
M. ornatus	100110000010110110 000110 0
M. persicae	000100021010001010 000100 1
M. varians	000000001010100110 000110 1
O. crataegarius	001100000100000110 111101 1
O. glechomae	100100001000010110 110001 1
O. insitus	001100001100000110 111101 1
O. inulae	011101101000110010 111101 1
O. leucocrini	031100101011102001 000100 1
O. malisuctus	011100001010100†0 011110 1
O. mentharius	†001000000001†0110 111001 1
O. phloxae	000100001111102011† 0†000† 1
O. reticulatus	030100021011102000 ????0? 1
O. valuliae	13010000101111120C0 000100 1

representing three of four subgenera, and 16% of the world fauna. These species were chosen to represent all possible subgenera, and are all the species of which adequate material was available. Three outgroup species were chosen from North American *Hyalomyzus*. The dataset is shown in Table 2.

Characters

Apterous viviparae

Head capsule:

1. Anterior setae on dorsum of head capsule: less than 0.5 times basal width of antennal segment III (0); more than 0.5 times basal width of antennal segment III (1).
2. Ornamentation on dorsum of head capsule: spinules or nodules present anteriorly and along margins, smooth in middle posteriorly (0); without spinules or nodules, sometimes with wrinkles (1); spinules or nodules entirely covering dorsum of head (2); dorsum of head with posterior surface in middle with polygonal reticulation (3) (Figs. 5–8).
3. Venter of head capsule adjacent to eyes: spinulose (0); smooth (1).
4. Ventral tubercles at rear of head capsule: present (0); absent (1).

Antenna:

5. Ratio of processus terminalis to the base of antennal segment VI: greater than 3 (0); less than 3 (1).
6. Venter of antennal segment II: bumpy (0); smooth (1).

Mouth Parts:

7. Pairs of setae on rostral segment III: almost always 2 (0); more than 2 (1).
8. Ultimate rostral segment: longer than hind tarsal segment II (0); shorter than hind tarsal segment II and without accessory setae (1); shorter than hind tarsal segment II and with accessory setae (2).
9. Number of setae on ultimate rostral seg-

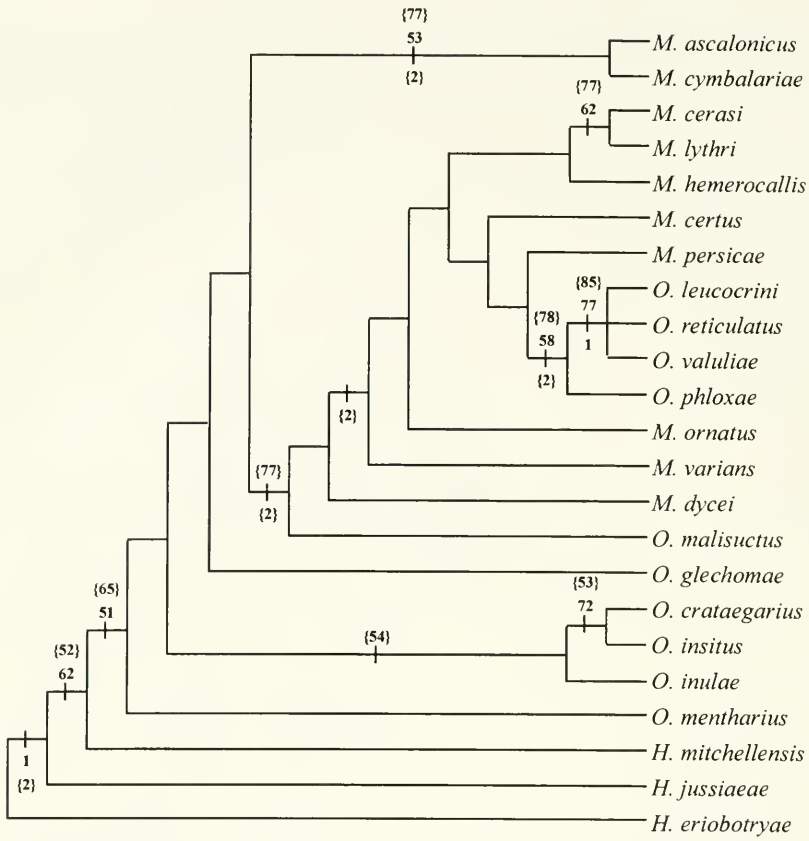


Fig. 1. Tree number one of two equally parsimonious trees found using the heuristic search option in PAUP with successively weighted data (weighted consistency index: 0.67; retention index: 0.84; and rescaled consistency index: 0.57). This tree was also one of 135 trees found using unweighted data (unweighted consistency index: 0.47; retention index: 0.64; and rescaled consistency index: 0.30). Numbers below some branches indicate branch support values from decay analyses, plain numbers indicating unweighted branch support, and numbers in braces indicating rescaled branch support from the weighted data (Bremer 1994). Numbers above branches display results of bootstrap analyses, plain numbers indicating results using unweighted data, and numbers in braces representing weighted data.

ment: 0–3 (usually 2) or rarely 4 accessory setae (0); usually 3 or more (rarely 2) accessory setae (1).

Legs:

10. Dorsal base of hind tibia: smooth or slightly wrinkled (0); distinctly scabrous or imbricated (1).
11. First tarsal segments chaetotaxy formula: 3–3-3 (0); 3–3–2 (1).

Abdomen:

12. Tergum patterning or sculpturing: maze-like with no distinct polygons, or irregular closed shapes with smooth space between them (0) (Fig. 3); smooth (1); pentagonal or hexagonal (2) (Fig. 4).
13. Spinal tubercles on abdominal tergite VII: usually present (0); absent (1).
14. Setae on abdominal tergite VIII: much shorter than basal width of antennal segment III (0); subequal to basal width of antennal segment III (1).
15. Shape of siphunculi: cylindrical or tapering (0); distinctly swollen (1); very slightly expanded near apex (2).

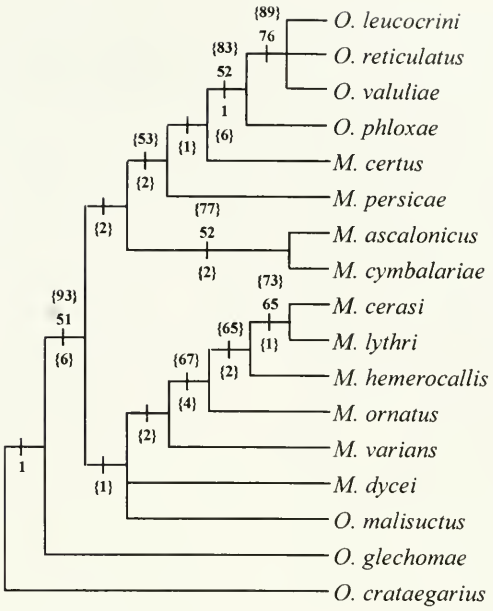


Fig. 2. Tree number one of four equally parsimonious trees found using the heuristic search option in PAUP with successively weighted data (weighted consistency index: 0.77; retention index: 0.84; and rescaled consistency index: 0.65). This tree was one of 14 trees found using unweighted data (unweighted consistency index: 0.47; retention index: 0.64; and rescaled consistency index: 0.30). Numbers below some branches indicate branch support values from decay analyses, plain numbers indicating unweighted branch support, and numbers in braces indicating rescaled branch support from the weighted data (Bremer 1994). Numbers above branches display results of bootstrap analyses, plain numbers indicating results using unweighted data, and numbers in braces representing weighted data.

16. Apical spinulation of cauda: entire, without blank spaces dorsally (0); reduced with blank spaces dorsally (1).
17. Abdominal tergum pigmentation: pigmented, with complete or nearly complete dorsal shield (0); pale, or with only cross bands on tergites VII and/or VIII.
18. Setae on cauda: 2 or 3 lateral pairs (0); 4 or more lateral pairs (1).

Alate viviparae

Antenna:

19. Secondary rhinaria on antennal segment V: absent (0); present (1).
20. Secondary rhinaria on antennal segment IV: absent (0); present (1).
21. Secondary rhinaria on antennal segment III: restricted to approximately half the circumference of the segment (0); distributed around the entire circumference of the segment (1).

Mouthparts:

22. Ornamentation of lateral part of mandible (base of mouthparts): spinulose or scabrous (0); smooth (1).

Abdomen:

23. Lateral abdominal tubercles: present in at least some specimens (0); absent (1).
24. Pigmented abdominal patch or bands: present (0); absent (1).

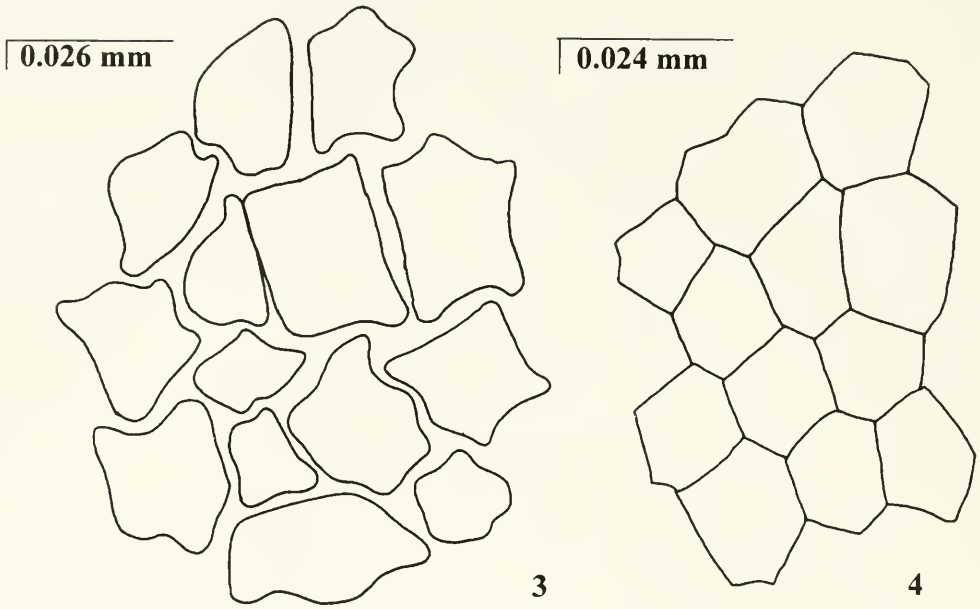
Nymphs

Legs:

25. Apical spinulation of hind tibia: present (0); absent (1).

Cladistics Results and Discussion

The full data set was analyzed using the heuristic search option in PAUP. One hun-



Figs. 3, 4. Dorsal sculpturing. 3, *Ovatus crataegarius.* 4, *Abstrusomyzus leucocrini.*

dred iterations of random addition sequence were performed, finding 135 equally parsimonious trees of length 91 steps. These had a consistency index (CI) of 0.47, retention index (RI) of 0.64, and rescaled consistency index (RC) of 0.30. One of these trees is presented in Fig. 1, with numbers below a few branches indicating results of a decay analysis (see Bremer 1994), and numbers above branches indicating the level of bootstrap support from 100 replications of heuristic bootstrap searching. Only branches supported by more than 50% of the bootstrap trees are labeled in Fig. 1. In all 135 trees, the group of four North American *Ovatus* is placed among the *Myzus* species, separate from other *Ovatus,* and supported by more than 50% of the bootstrap trees. Old World *Ovatus* are placed as close relatives to the outgroup *Hyalomyzus.* The close relationship between *Ovatus* and *Hyalomyzus* has been discussed by Eastop (1966), Nielsson and Habeck (1971), and Blackman and Eastop (1994).

The four North American *Ovatus* formed a clade in all 135 trees and were often placed with *M. certus* and *M. persicae,* two species with swollen siphunculi that represent the subgenus *Nectarosiphon.* Moving the four North American species from within *Myzus* to the more basal parts of the tree along with the other *Ovatus* caused an increase in tree length of three or four steps, depending on the branch to which they were attached. For example, moving the branch composed of these four species to become the terminal *Ovatus,* along with *Ovatus malisuctus* (Matsumura), caused an increase in tree length of three steps. But it is clear from the bootstrap results that the most strongly supported clade of more than two species is that composed of the four North American species related to *O. phloxae,* henceforth referred to as the "*phloxae* group."

A successive weighting procedure using the default settings in PAUP was conducted, finding two of the 135 trees found using unweighted data, with the following weighted statistics: length, 22, 140; CI, 0.67; RI, 0.84; RC, 0.57. The tree shown in Fig. 1 is one of these trees. Bootstrap and decay analyses were performed using the weighted dataset, and their results are dis-

played in Fig. 1. Decay indices in braces in Fig. 1 are rescaled (Bremer 1994). The two successive weighting trees even more strongly support the monophyly of the *phloxae* group and its separation from Palearctic *Ovatus*. Monophyly of the *phloxae* group was supported in 78% of the bootstrap trees and through 2 rescaled steps of decay.

The results of this analysis clearly indicate that the *phloxae* group does not belong to *Ovatus*. Consistent placement of the *phloxae* group within the clade of *Myzus* species indicates that they are more closely related to *Myzus* than they are to *Ovatus* of the Palearctic. It should also be pointed out that *O. malisuctus* is placed among the *Myzus* clade in some of the 135 trees, and may be more closely related to *Myzus* than are the other *Ovatus*. Further studies focusing on Palearctic aphids in and related to *Ovatus* will be required to finalize the classification of this and other problematic species not included in this study.

The unique characters of the four North American *"Ovatus"* species (peculiar siphuncular shape, generally more setose rostrum and cauda, reticulate tergum) may justify the erection of a new genus. Therefore, another analysis was conducted focusing only on the relationship of these four species to the *Myzus* included in the analysis. The objective of this analysis was to determine whether the *phloxae* group and the available *Myzus* species would form separate monophyletic groups. The same set of characters was used. Three Palearctic *Ovatus* were included, the first two as outgroup taxa: *O. crataegarius, Ovatus glechomae* Hille Ris Lambers, and *O. malisuctus*. Ingroup species were the *phloxae* group, and all ten *Myzus* in the first analysis.

A "branch and bound" search found fourteen trees of length 71, with a CI of 0.55, RI of 0.56, and RC of 0.31. One of these trees is presented in Fig. 2. Similar to the previous analysis, the *phloxae* group is part of a clade with two *Myzus (Nectarosiphon)* species. These *Myzus* have swollen siphunculi and, similar to the *phloxae* group, two setae on the first segment of the hind tarsus. Rearranging the trees to make the *phloxae* group and *Myzus* monophyletic requires only a two step increase in tree length. A successive weighting analysis was conducted, which selected four of the original fourteen trees of length 71 (weighted statistics: length, 19, 611; CI, 0.77; RI, 0.84; RC, 0.65). The tree in Fig. 2 is one of these trees. The results of weighted and unweighted decay and bootstrap (500 replications) analyses are presented in Fig. 2 as well. Unweighted data supported the unity of the *phloxae* group through 1 step of decay and in 52% of the bootstrap trees. Few branches were strongly supported by either measure using unweighted data. Weighted data yielded very strong support for the *phloxae* group, which held up through six steps of rescaled decay and was present in 83% of the bootstrap trees.

These results point to the necessity for the erection of a new genus to house the *phloxae* group. First of all, it is clear that the *phloxae* group is not congeneric with *Ovatus* from the Palearctic. The full analysis that used *Hyalomyzus* as outgroup was overall rather weak, but where it was relatively strong was in the separation between the basal *Hyalomyzus/Ovatus* clade and the more apical *Myzus/phloxae* group clade. This showed that the *phloxae* group is more closely related to *Myzus* than to Palearctic *Ovatus*. The next step in the analysis examined more closely the relationship between the *phloxae* group and the other *Myzus*. The results showed that there was strong support for the monophyly of the *phloxae* group, but not for the relationship between it and the *Myzus* with which it was placed in the trees. Thus not only is there no support for the placement of the *phloxae* group in *Ovatus*, but the group also appears to be only weakly related to any species of *Myzus*. Our cladistic results as well as the peculiar morphology of the *phloxae* group provide ample justification for the erection of a new genus, as we do below.

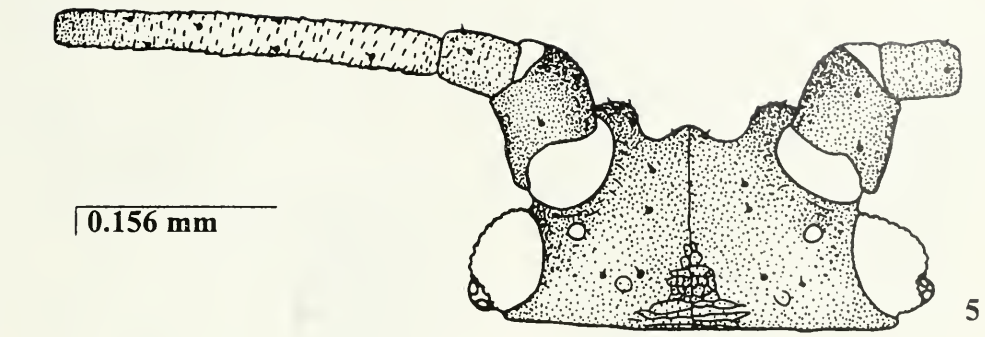
Abstrusomyzus Jensen and Stoetzel, new genus

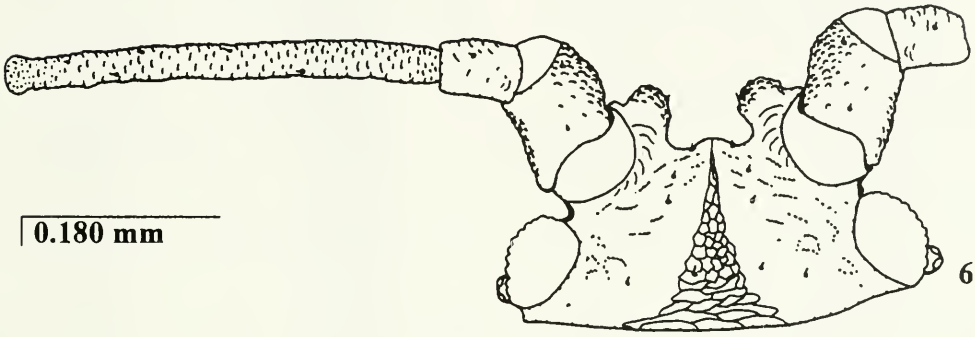
(Figs. 4–18)

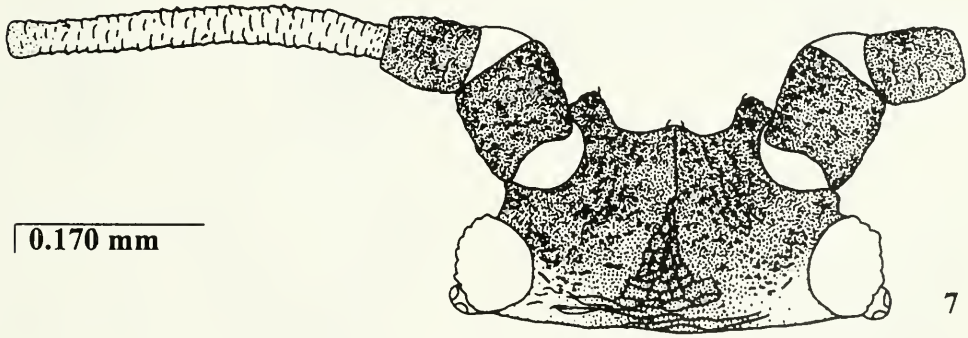
Type species: *Phorodon phloxae* Sampson

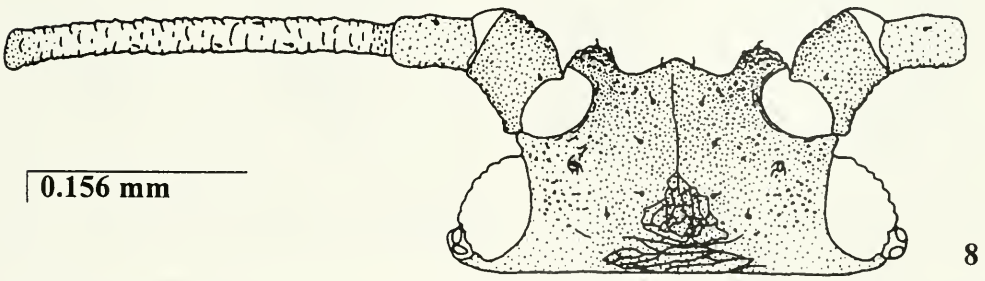
Diagnosis.—*Abstrusomyzus* can be separated from *Ovatus, Myzus* and other *Myzus*-like genera in North America by the peculiar shape of the siphunculi in all stages (Figs. 9–12), the distinctly pentagonal/hexagonal reticulated pattern of the tergum (Fig. 4), 3,3,2 first tarsal segment chaetotaxy, and the usual presence of pigmented cross-bands on the abdomen of alate viviparae (Figs. 17, 18). The completely pigmented tergum in apterous viviparae of the three species other than *A. phloxae* is also unusual. One North American species that may be closely related to *Abstrusomyzus* is *Aphthargelia symphoricarpi* (Thomas). The latter species shares with *Abstrusomyzus* the same type of dorsal reticulate sculpturing, moderately prominent *Myzus*-like antennal tubercles, a relatively large number of caudal setae, large lateral tubercles, and dark transverse abdominal bands in the alate viviparae. *Abstrusomyzus* and *A. symphoricarpi* differ significantly, in that the latter species has 3,3,3 first tarsal chaetotaxy, very short almost barrel-shaped siphunculi, and more numerous secondary rhinaria on antennal segments III-V.

Description.—*Apterous vivipara:* Nymph: hind tibiae of nymphs without spinules apically. Adult: body length 0.83–1.94 mm. Dorsum of head capsule (Figs. 5–8) pale to black, with small sparse spinules often arranged in curving rows. Spinal region of head capsule with more or less triangular area of reticulate sculpturing; spinal tubercles sometimes present. Dorsum of head normally with 4 setae in posterior row, with 3 pairs farther forward; small lateral ocelli or traces thereof often present. Antennal tubercles moderately to strongly produced, rough, with several setae. Frons often produced slightly as a median tubercle. Setae on head short, blunt, much shorter than basal width of antennal segment III. Eyes normal, with ocular tubercles and interfacetal spaces brownish pigmented. Ventral surface of head capsule more or less evenly, but sometimes very lightly, spinulose, with spinules often arranged in rows. Antennal tubercles with large ventral projections bearing a few short setae. Ventral head setae sometimes as short as the dorsal setae, sometimes about twice as long. Mandibular area of mouthparts smooth. Antennae normally shorter than body; antennal segment I rough, roughest medially, with several setae, these about equal in length to those on dorsum of head capsule; antennal segment II rough, roughest ventrally and medially, with course imbrications; antennal segment III covered with imbrications, rarely with 1 or 2 secondary rhinaria; remainder of antenna roughly imbricated. Rostrum reaching middle of thorax, with segment II strongly ornamented with rows of spinules; segment III with 2 pairs of setae, these located in apical ½; ultimate rostral segment about equal in length to tarsal segments II, or about 0.1 mm, with 3–9 accessory setae. Pronotum with 3 pairs of short setae: 1 spinal, 1 pleural, and 1 lateral; the lateral pair associated with a frequently present pair of lateral tubercles that are sometimes bi- or trifid; setae about equal in length to those on the dorsum of the head. Surface of pronotum reticulate, the reticulations usually somewhat flattened front to back. Meso- and metathoracic terga reticulate and often pigmented, setae extremely short, blunt. Coxae of all legs covered with spinulose imbrications. Femora with sparse imbrications, especially anteriorly, with setae about equal in length to dorsal head setae. Tibiae sparsely setose, basal setae much shorter than those at apex. First tarsal segments with 3,3,2 setae (i.e., hind tarsus I with 2 setae), second tarsal segments imbricated. Mesothoracic furca sessile or with short stalk. Abdomen with tergum reticulate throughout, sometimes pigmented. Dorsal abdominal setae blunt, very short, except sometimes longer on tergite VIII. Abdominal segments II–VI often with lateral tu-

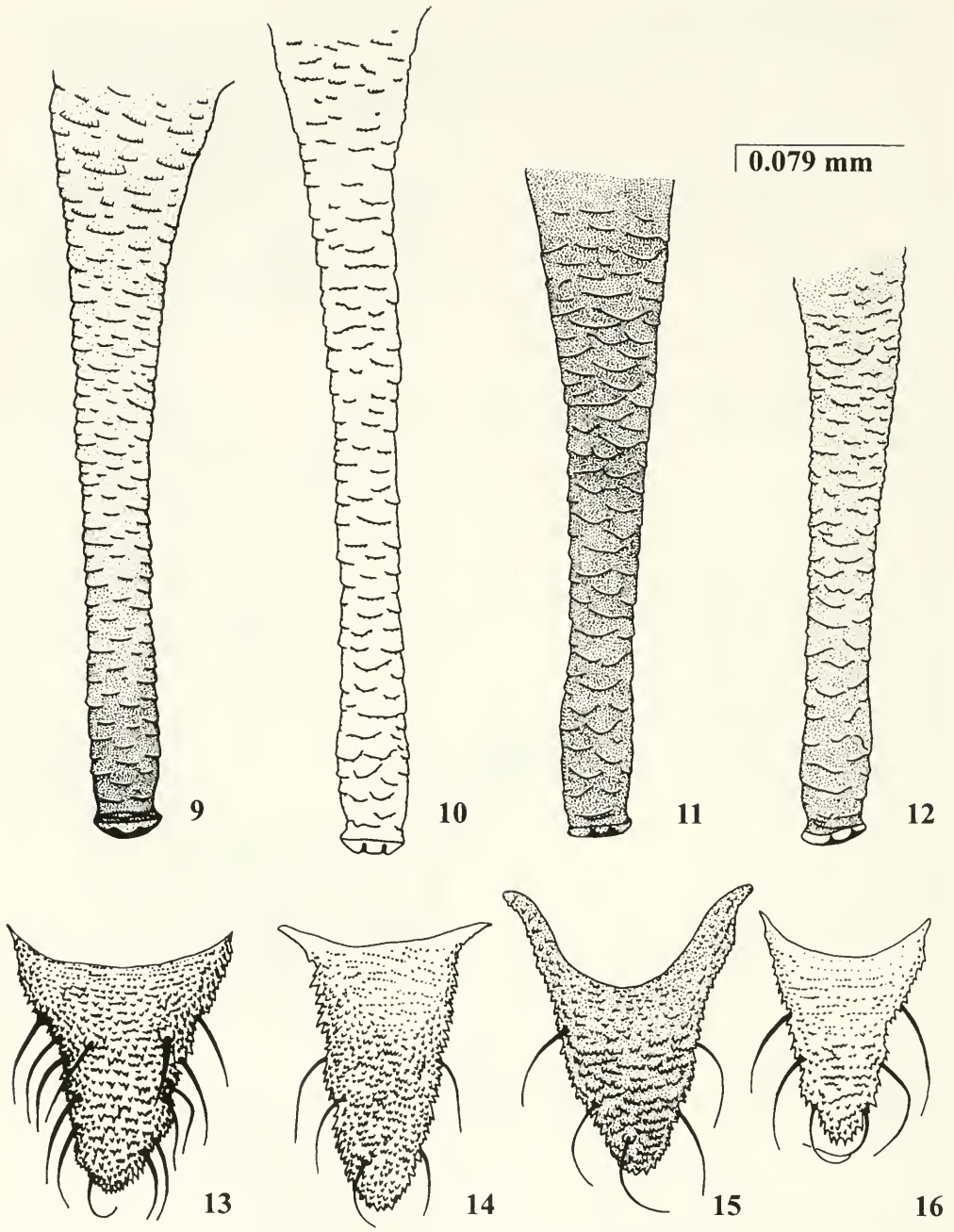






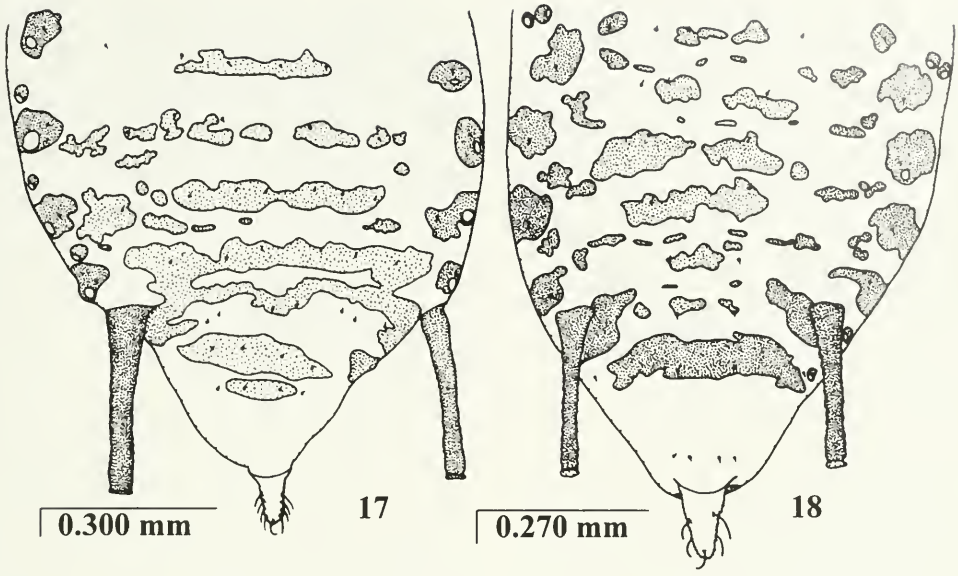


Figs. 5–8. Head with first three antennal segments of apterous viviparae. 5, *Abstrusomyzus leucocrini*. 6, *A. phloxae*. 7, *A. reticulatus*. 8, *A. valuliae*.



Figs. 9–16. Siphunculi and caudas of apterous viviparae. 9, 13, *Abstrusomyzus leucocrini*. 10, 14, *A. phloxae*. 11, 15, *A. reticulatus*. 12, 16, *A. valuliae*.

bercles of various sizes. Siphunculus cylindrical over most of its length, slightly swollen toward the tip (Figs. 9–12), imbricated throughout. Cauda moderately long, with 4–15 setae, more or less pointed apically. Tergite VIII with 4–7 setae, normally 4. Ventral abdominal setae pointed. Gonapophyses 3 in number.



Figs. 17, 18. Abdominal tergum of alate viviparae. 17, *Abstrusomyzus leucocrini.* 18, *A. phloxae.*

Alate vivipara: Body length 0.98–1.92 mm. Head capsule dark, slightly wrinkled or smooth, not reticulate. Lateral and median ocelli present, median ocellus creating a strong median tubercle. Antennal tubercles only slightly rough, with several setae. Ventral surface of head capsule more or less smooth, sometimes with a few sparse spinules. Antennal segment III with secondary rhinaria scattered over most or all of its length, limited to one side, normally less than 20 in number; antennal segment IV occasionally with a few secondary rhinaria; antennal segment V without secondary rhinaria. Thoracic tergites smooth. Sclerites of thorax dark brown, of normal design. Abdomen with dark lateral sclerites, and often dark cross bands on some segments. Dark abdominal cross bands often reticulate in a similar fashion to the tergum of apterous vivipara. Otherwise essentially as in apterous vivipara.

Etymology.—The generic name is taken from the Latin word "abstrusus," meaning hidden or concealed and *Myzus,* which is based on the Greek "myzo," meaning suck. The name is meant to draw attention to the way the type species of the genus is often hidden in ant-created shelters or on the lower leaves of its host plants. The gender is masculine.

Key to Apterous Viviparae of *Abstrusomyzus*

1. Dorsum of apterous vivipara unpigmented; antennal tubercles strong, with prominent converging processes (Fig. 6); dorsum with hexagonal reticulation usually faint due to the pale, unsclerotized tergum . . . . . *Abstrusomyzus phloxae* (Sampson)
– Dorsum of abdomen of apterous vivipara dark pigmented, usually black; antennal tubercles strong, but without converging processes (Fig. 5, 7, 8); dorsum with distinct hexagonal reticulation (Fig. 4) 2
2. Apterous vivipara without traces of lateral ocelli, and without spinal tubercles on head; antennal segments I & II nearly black, antennal segment III unpigmented, except extreme tip slightly dusky; dorsum entirely dark, concolorous with cauda and siphunculus . . . . . *Abstrusomyzus reticulatus* (Heie)
– Apterous vivipara usually with traces of lateral ocelli, and sometimes with low spinal tubercles on head; antennal segment I brown, antennal segment II much paler than I, antennal segment III with tip brown; dorsum entirely dark or

with some pale areas, cauda and siphunculus pigmentation variable 3

3. Tergite VIII with middle pair of setae pointed, about twice as long as lateral pair of setae on tergite VIII, and about three times as long as setae on tergite VII; cauda usually with fewer than 9 setae (Fig. 16) . . . . . *Abstrusomyzus valuliae* (Robinson)

– Tergite VIII with middle pair of setae blunt, about equal in length to the lateral pair on tergite VIII and those on tergite VII; cauda usually with more than 9 setae (Fig. 13) . . . . . *Abstrusomyzus leucocrini* (Gillette and Palmer)

Key to Known Alate Viviparae of *Abstrusomyzus*

1. Setae on abdominal tergite VIII distinctly longer than setae on tergite VII, and about equal to basal width of antennal segment III; lateral tubercles small or absent . . . . . *Abstrusomyzus valuliae* (Robinson)

– Setae on abdominal tergite VIII about equal in length to the setae on abdominal tergite VII, and much shorter than the basal width of antennal segment III; lateral tubercles various . . 2

2. Cauda relatively setose, usually with more than 9 setae; lateral abdominal tubercles relatively large (Fig. 17); antennal tubercles moderately prominent as in Fig. 5 . . . . . *Abstrusomyzus leucocrini* (Gillette and Palmer)

– Cauda usually with fewer than 9 setae; lateral abdominal tubercles small or absent (Fig. 18); antennal tubercles sometimes strongly produced similar to the apterous vivipara (Fig. 6) . . . . . *Abstrusomyzus phloxae* (Sampson)

Abstrusomyzus leucocrini (Gillette and Palmer 1929), **new combination**
(Figs. 4, 5, 9, 13, 17)

Myzus leucocrini Gillette and Palmer 1929: 470; Gillette and Palmer 1934: 202; Palmer 1952: 338.

Ovatus leucocrini: Eastop and Hille Ris Lambers 1976: 328; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

This species was described from several collections made by L.C. Bragg from Fort Collins, Colorado, in May of 1916. The aphids were found on *Leucocrinum montanum,* a small herb of the Liliaceae. We know of no other collections of this aphid from *Leucocrinum.* There are a few individual alate viviparae found in traps and on various plants that seem to be this species, but lack of good host plant records makes any deductions about the biology of this species difficult. The presence of many apterous and alate viviparae on an herb (*Leucocrinum*) in May suggests a monoecious life cycle. Further collecting will be needed to determine whether this species is monophagous on *Leucocrinum,* or feeds on other plants as well.

Within *Abstrusomyzus,* this species is most similar to *A. reticulatus* and *A. valuliae.* In the material at hand (19 apterous, and 15 alate viviparae), the apterous viviparae of *A. leucocrini* almost always have partially developed lateral ocelli, and often spinal tubercles on the head as well (Fig. 5). *Abstrusomyzus reticulatus* lacks both of these, and *A. valuliae* always lacks the latter, but usually lacks both. The cauda of *A. leucocrini* is usually more setose, ranging from 9–15 setae in both alate and apterous viviparae, compared to 4–9 setae on the cauda (Figs. 13, 15, 16) of the other two species. This species and *A. phloxae* have characteristic brown to orange regions of pigmentation surrounding the bases of the siphunculi. It is not known whether the other two species in the group have this unusual pigmentation pattern. Differences between *A. leucocrini* and *A. phloxae* are discussed under the latter species. Adequate descriptions of this species have been published previously (Mason 1940, Palmer 1952).

Types of this species are located in the USNM. A single paratype slide was also obtained on loan from the BMNH, and another from UCB. Other material examined were specimens from the same series as the types, some of which were cleared and remounted for this study.

Abstrusomyzus phloxae (Sampson 1939), **new combination**
(Figs. 6, 10, 14, 18)

Phorodon phloxae Sampson 1939: 174.

Myzus plantagineus Passerini (misidentifi-

cation): Williams 1911: 65; Davis 1910: 495; Davis 1911: 23; Mason 1940: 17.
Ovatus phloxae: Hille Ris Lambers 1966: 600; Heie 1972: 450; Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

Abstrusomyzus phloxae was described from California based on specimens collected on *Phlox subulata.* Sampson described the species in *Phorodon* Passerini under a broad concept of the genus that included species that are today considered *Ovatus* and *Myzus.* Since Sampson (1939), the species has been collected on many other plants (Table 1). In the eastern half of the U.S.A., *A. phloxae* is most often found on the crown, young leaves, and roots of *Plantago major.* This led to the misidentification of this species by Williams (1911) and Mason (1940) as *Myzus plantagineus* Passerini. Hille Ris Lambers (1966) was the first to understand the identity and wide host range of this species.

This species has been found on many unrelated host plants, but mostly only in isolated collections. It has been best studied in eastern U.S.A. on *Plantago major.* It was collected on this plant in Illinois, Maryland, Nebraska, Pennsylvania, and Virginia in May, June, and July of various years. When feeding on this plant *A. phloxae* is often tended by ants (*Lasius alienus* Foerster in Maryland) which build earthen "tents" surrounding the young leaves on which the aphids feed. Such "tents" we found in Maryland housed a mixture of aphids, including *A. phloxae, Aphis gossypii,* and *Nearctaphis bakeri* (Cowen). We reared *A. phloxae* on *Plantago* on potted plants indoors. To test acceptance of two host plants used by other *Abstrusomyzus* species, we allowed the population of *A. phloxae* on *Plantago* to increase, and provided *Fragaria* sp. (the host genus of *A. valuliae)* and *Oxalis* sp. (the host genus of *A. reticulatus)* in adjacent potted plants. Many *A. phloxae* individuals attempted to colonize *Fragaria* and *Oxalis,* but no colonies were established during the two weeks of attempts. The *A. phloxae* population eventually killed its host plants. This bolstered the somewhat weak morphological separation between *A. phloxae* and *A. reticulatus* and *A. valuliae,* since despite the polyphagy of *A. phloxae,* it was unable to colonize the hosts of these two species. The aphids reared on potted plants were heavily parasitized by the aphelinid *Aphelinus asychis* Walker.

Little is known about the life history of this species. It has been collected in every month except October and November. In Maryland the earliest collection was February. In Oregon it is most commonly found in August and September. The single known collection of oviparae was found in Abbotsford, British Columbia on 2 January 1992. Given that males have never been found, and considering that it has been collected almost throughout the year, we suspect that *A. phloxae* is primarily anholocyclic. Concerted collecting efforts during autumn and winter will be required to determine the life history of this species.

When *A. phloxae* is found in nature, it almost always lives on the lower leaves of its host plant, and generally on plants that are low to the ground or have a basal rosette. When reared on potted plants indoors, the aphid thrived on all parts of the plant, but moved to the upper parts only when populations were very large. This propensity for living near the ground, but on many different plant species, suggests that this aphid may be a rare example of a habitat-specific, rather than host-specific aphid. Other examples of this phenomenon are known in the aphids, such as the polyphagous tree feeding aphid *Longistigma caryae* (Harris), which feeds specifically on bark, and *Rhopalosiphum nymphaeae,* which feeds on aquatic herbs.

Chromosome number is often useful as a taxonomic character in aphids. For most species of *Myzus* in which it is known, the chromosome number is 2n = 12, with a few having 2n = 13 or 14. One slide obtained

on loan from the BMNH contains a sample of apterous viviparae of *A. phloxae* that was karyotyped as 2n = 18 by R.L. Blackman. Karyotyping of the other *Abstrusomyzus* species may show that chromosome numbers will also support the separation of *Abstrusomyzus* from similar *Myzus*-like genera.

Within *Abstrusomyzus,* apterous viviparae of *A. phloxae* are easily recognized by their pale tergum and large, distinctly converging antennal tubercles (Fig. 6). Alate viviparae are far more difficult to separate from other members of the group. The alate form of *A. reticulatus* is unknown. The long middle pair of setae on abdominal tergite VIII is diagnostic for *A. valuliae.* This leaves *A. leucocrini* as the primary species that may be confused with *A. phloxae* in the alate stage. *Abstrusomyzus phloxae* has relatively more prominent antennal tubercles, and usually has fewer caudal setae; *A. phloxae* normally has eight or fewer caudal setae (but sometimes up to 10), compared to 9–13 in *A. leucocrini* (Figs. 13, 14). Many *A. leucocrini* have spinal tubercles on the head, which are always absent in *A. phloxae.* Finally, *A. phloxae* tends to have smaller lateral tubercles, and often fainter or less extensive abdominal pigmentation (Figs. 17, 18). Good descriptions of *A. phloxae* can be found in Sampson (1939) and Mason (1940).

Many paratypes of this species were seen, having been borrowed from the UCB. Other material examined included material from all the host plants and states listed for this species in Table 1. Seventy eight apterous viviparae, and 59 alate viviparae were seen during this study.

Abstrusomyzus reticulatus (Heie 1972), **new combination**
(Figs. 7, 11, 15)

Ovatus reticulatus Heie 1972: 447; Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

This species was described based on nine specimens collected on *Oxalis ?stricta* in North Carolina. These specimens are still the only ones known for the species. They include seven apterous viviparae, one ovipara, and one brachypterous male.

Abstrusomyzus reticulatus is apparently monoecious holocyclic based on the occurrence of viviparae, a male, and ovipara together on the herbaceous *Oxalis.* According to Heie (1972) the aphids cause the leaves of *Oxalis* to curl. Further collecting will be required to determine the host range of this species.

This species can be distinguished from *A. phloxae* as described above. *Abstrusomyzus valuliae* is distinct from this species and others in the group because of the long setae on abdominal tergite VIII. *Abstrusomyzus reticulatus* is most similar to *A. leucocrini.* These species can be separated based on the small number of caudal setae in *A. reticulatus,* its complete lack of spinal tubercles on the head, and relatively dark antennal segment II. This is the only species of *Abstrusomyzus* for which the male is known. The brachypterous condition of the single known male is probably aberrant. Heie (1972) provides good descriptions of all known morphs.

Types of this species are housed in the USNM (holotype, one paratype), BMNH (3 apterous vivipara paratypes), C.F. Smith collection (two apterous viviparae, not seen), and in the collection of O.E. Heie (one apterous vivipara and one ovipara, not seen).

Abstrusomyzus valuliae (Robinson, 1974), **new combination**
(Figs. 8, 12, 16)

Myzus valuliae Robinson 1974: 469.

Ovatus valuliae: Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 226; Remaudière and Remaudière 1997: 135.

Abstrusomyzus valuliae is known only from the material used by Robinson for the description of the species from Manitoba,

Canada. It was collected several times during the summer of 1973 and once in the spring of 1974 on *Fragaria vesca,* wild strawberry. These specimens include many apterous and alate viviparae.

Little is known about the biology of this species. It is most likely monoecious, but host plant range is unknown. When on *Fragaria,* the aphids cause the leaves to curl tightly, and the aphids feed inside the curled leaves (Robinson 1974).

This species can be distinguished from *A. phloxae* as described under that species. Among the three darkly pigmented species of *Abstrusomyzus,* this species can be most easily distinguished by the long middle pair of setae on the abdominal tergite VIII. It is most similar to *A. leucocrini,* both species frequently having lateral ocelli or traces thereof in the apterous vivipara. Robinson (1974) described this species thoroughly.

The holotype of *A. valuliae,* which we did not see, was deposited in the Canadian National Collection, Ottawa. Paratypes were deposited in the Canadian National Collection, BMNH, and the USNM. Many paratypes and some additional material from the same collections were examined for this study.

Status of *Ovatus*

The removal of four species from *Ovatus* leaves only a single species of the genus in North America, *O. crataegarius.* This species can be separated from *Myzus* found in North America by its lack of spinules on the hind tibia of nymphs, the lack of a dorsal pigmented abdominal patch in the alate viviparae, and the presence of many secondary rhinaria on antennal segments III, IV, and V in alate viviparae. *Ovatus crataegarius* can be separated from another somewhat similar species, *Phorodon humuli* (Schrank), by its first tarsal chaetotaxy of 3,3,3, lack of pigmented abdominal patch in the alate viviparae, and its antennal tubercles, which are strongly convergent, but lack the extremely prominent finger-like process of *Phorodon.* The primary way that *Ovatus* is separated from *Hyalomyzus* is the swollen siphunculi of the latter genus. An excellent diagnosis for the genus *Ovatus,* as it is understood here, is provided by Heie (1994) (i.e., Heie's diagnosis does not address the characters of the four species here placed in *Abstrusomyzus*).

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THE LARVAL INSTARS OF THE WHEAT MIDGE, *SITODIPLOSIS MOSELLANA* (GÉHIN) (DIPTERA: CECIDOMYIIDAE)

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Abstract.—The wheat midge, *Sitodiplosis mosellana* (Géhin), is shown to have three larval instars. Each instar is described and illustrated, the initial instar for the first time. An alleged synonym of the wheat midge, *Cecidomyia amyotii* Fitch, is removed from synonymy with the wheat midge and considered a dubious name.

Key Words: wheat midge, *Sitodiplosis,* larva

The wheat midge, *Sitodiplosis mosellana* (Géhin), is one of the two most important cecidomyiid pests of wheat in North America, the other being the Hessian fly, *Mayetiola destructor* (Say). Originally from the Palearctic Region, both are now well established in North America. All three larval instars of the Hessian fly have been described in detail (Gagné and Hatchett 1989), but those of the wheat midge are less well known, and its first instar has not previously been described.

The general life history of the wheat midge or, in the United Kingdom, the orange wheat blossom midge, has been summarized by Reeher (1945) and Barnes (1956), and more information on certain aspects of its attack and feeding were treated by Mukerji et al. (1988) and Elliott and Mann (1996). Females lay eggs on emerging spikes of wheat before anthesis. Upon hatching, the larvae crawl to and settle upon the developing flower parts, where they feed and interfere with the proper development of the kernels. The full grown larva eventually drops from the wheat head, crawls into the soil, and constructs a silk cocoon in which the larva overwinters.

We show that the wheat midge has three larval instars, as do the Hessian fly and all other cecidomyiids that have been carefully studied (Gagné 1989). Upon hatching, the first instar of the wheat midge crawls to a feeding site on the developing wheat grain, settles, and begins to feed. Within two to three days the larva molts to the second instar, which continues to feed and grow until the third instar begins to develop. The second instar skin then becomes brittle and serves as a temporary cocoon for the third instar, which does not feed. The fully developed third instar can exit from the second instar skin immediately but may stay within this skin on the kernel for several weeks. Upon leaving the temporary cocoon, the third instar drops to the ground and burrows into the soil where it spins its cocoon.

In most other cecidomyiids the second instar skin is shed as soon as the third instar is fully developed and, in gall-making species, can be found crumpled in a compact mass at the caudal end of the third

instar. The situation in the wheat midge is somewhat analogous to that of the Hessian fly in which the second instar skin also serves as a cocoon for the non-feeding third instar, with the difference that the third instar of the Hessian fly pupates there also. Because the Hessian fly feeds head groundwards between the culm and leaf sheath, the third instar has to reverse position from head to tail within the second instar skin. In this way the pupa of the Hessian fly is positioned so that adults are able to exit from the wheat sheaths. The third instar of the wheat midge is not so constrained, so does not need to reverse its position within the second instar skin. These two cecidomyiids on grasses are not closely related, each belonging to a different supertribe, so this rare development of a brittle second instar skin as a puparium or larvarium has evidently evolved separately. A puparium is present also in another grass-infesting gall midge, the sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Solinas 1986), which belongs to the same supertribe but to a different tribe than the wheat midge. A puparium is also known for other gall midges that do not occur on grasses but is still rare. Examples are *Thurauia aquatica* Rübsaamen from sedges in Europe and an undescribed species that belongs to no known genus from maple seeds in Japan.

The description and figures that follow will allow recognition of each of the three instars of the wheat midge. They are necessary to correct misinformation in Borkent (1989) that was based on mixed series of three species and in which it was asserted that the wheat midge had four instars.

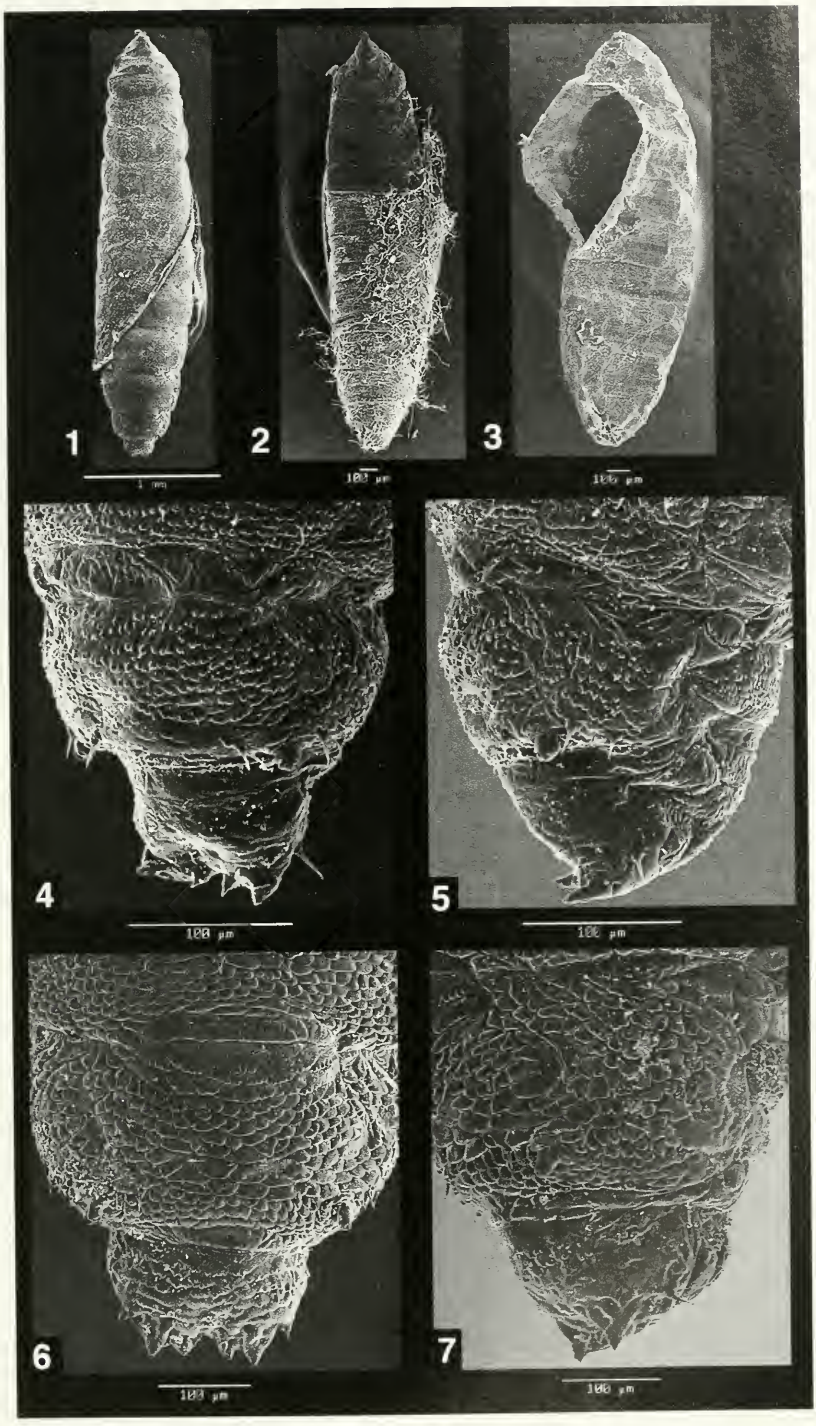
Methods

In 1997, collections of wheat heads (cultivar Roblin) were made by one of us (JFD) from a plot area (latitude 52.1951, longitude 106.1071) near St. Denis, a hamlet about 26 miles east of Saskatoon, Saskatchewan, Canada. Twenty-five primary heads were collected at intervals of 1 or 2 days from July 7 until July 18 and then at intervals of 3 to 4 days until July 31. The first eggs were found on the outside of the glumes on July 7 and the first newly hatched larvae on July 9. The larvae were removed from the heads and preserved in 70% alcohol for subsequent examination. Some specimens were mounted on microscope slides using the method outlined in Gagné (1989); earlier instars were mounted in Hoyer's medium because of their small size and the risk of their being lost in the various steps involved in balsam mounting. Terminology for larval morphology follows that in Gagné (1989).

Description of Larval Instars of *Sitodiplosis mosellana*

The first instar differs markedly from the remaining instars. It has only one pair of functional spiracles (Figs. 10, 12), which are situated on the eighth abdominal segment and are relatively large in relation to body size compared to the eighth abdominal spiracle of other instars (Fig. 13). Its cuticle is entirely smooth except for several horizontal rows of tiny spicules dorsally and ventrally near the anterior part of most segments (Figs. 11, 12). The second and third instars each have spiracles on the first thoracic and on the first through eighth abdominal segments. The cuticle of the second and third instars is rough, covered almost entirely by raised scale-like bumps (Figs. 4–7). The third instar differs from the second in having a spatula, the clove-shaped dermal structure on the venter of the prothorax (Fig. 9). Because this structure begins to develop while the third instar is still encased in the second instar, the spatula is usually visible through the skin of older second instars. An additional difference between the second and third instars is that the two caudalmost terminal papillae are more equal in size in the third instar than in the second (Fig. 14). A more detailed description follows:

First instar (Figs. 10–12).—Body length 0.45–1.05 mm. Antenna three times as long

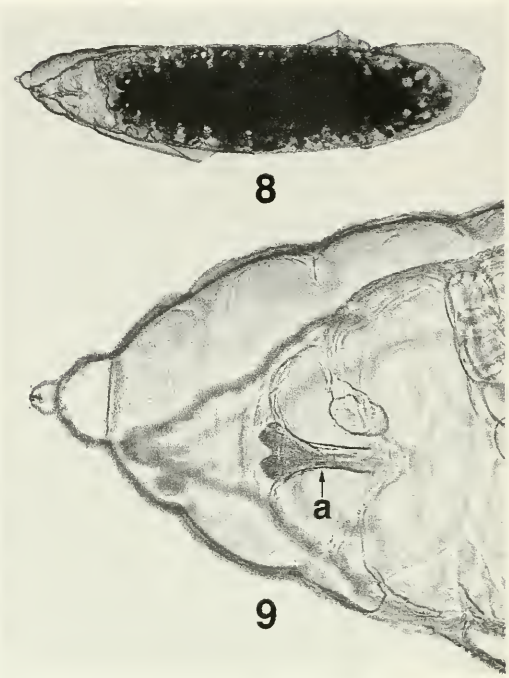


Figs. 1–7. *Sitodiplosis mosellana.* 1–3, Brittle second instar skins from which third instar is emerging (1, 2) or has emerged (3). 4, Second instar (dorsolateral). 5, Same (lateral). 6, Third instar (dorsal). 7, Same (lateral).

as wide. Two pairs of spiracles apparent, one on prothoracic segment, the other on eighth abdominal segment: prothoracic pair evident only as short projection, evidently not functional; posterior pair prominent, with three acute apical projections. Cuticle smooth except for several horizontal rows of tiny spicules dorsally and ventrally near anterior part of each segment except for prothorax. Pattern and number of papillae basic for supertribe Cecidomyiidi, their setae mostly very short, dorsal and pleural papillae of eighth segment slightly longer than preceding segments, and terminal papillae modified as follows: one dorsal, subcaudal pair with short setae not surpassing length of those on preceding segments; one lateral pair with elongate setae several times longer than subcaudal pair; two caudal pairs with stout, wide setae, the outer of these two pairs more than twice length of inner pair.

Second instar (Figs. 4, 5, 8, 9, 14).—Body length 1.05–3.30 mm. Antenna about twice as long as wide. Spiracles present on prothoracic and first through eighth abdominal segments, eighth abdominal pair slightly larger than preceding spiracles, none with apical projections. Cuticle rugose, covered almost completely with raised scale-like bumps, these much smaller and arranged in several regular anteroventral horizontal rows on mesothoracic to eighth abdominal segments. Pattern of papillae similar to that of first instar but setae more conspicuous. Terminal papillae modified as follows: two lateralmost papillae with setae, the more ventral pair with longer setae; two pairs with stout setae, the inner pair with setae noticeably thinner than outer pair.

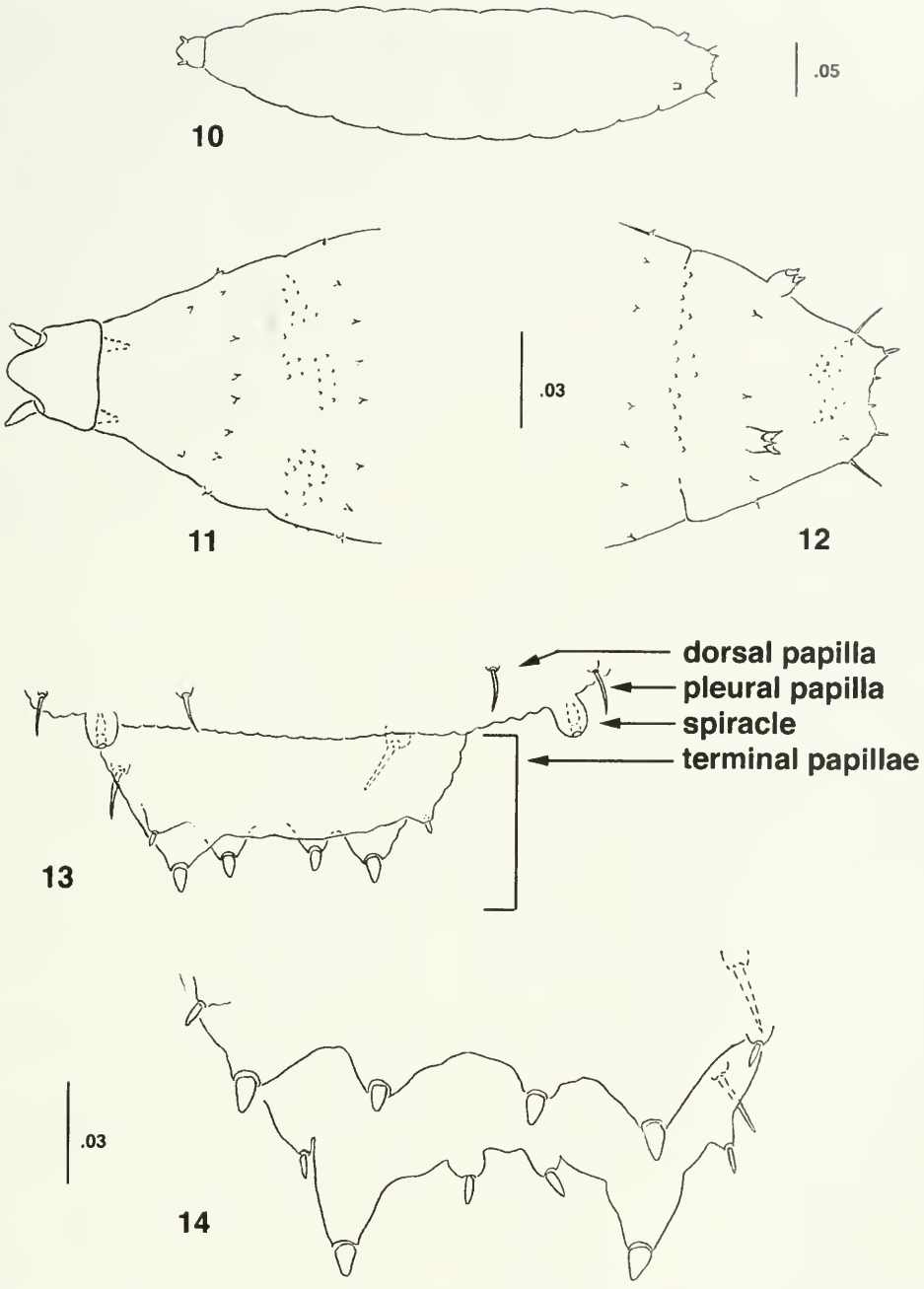
Third instar (Figs. 6–9, 13, 14).—Body length 2.80–3.20 mm. Antenna and spiracles as for second instar. Cuticle also as for second instar except for presence of ventral prothoracic spatula and horizontal anteroventral rows of bumps more numerous and more extensive. Pattern of papillae similar to that of second instar. Terminal papillae modified as for second instar except inner pair of caudal, stout setae more nearly equal in size to outer pair.



Figs. 8, 9. *Sitodiplosis mosellana*. 8, Third instar inside second instar skin (ventral). 9, Detail of same (a = spatula).

Remarks.—Borkent (1989) described and illustrated four alleged instars for the wheat midge, each with a spatula. The first instar of that paper is a third instar of an undetermined *Clinodiplosis* sp. Its posterior abdominal segment, as illustrated in his Fig. 2A, has three of the four pairs of terminal papillae corniform (short and stout) and only one pair setiform, characteristic of species of *Clinodiplosis*. The presence of a spatula indicates that the specimen is a third instar. Specimens of these larvae occasionally are found in association with wheat midge larvae. Representatives of this species in the USNM are curated with wheat midge larvae until adults are reared and the species can be identified further.

The second instar of Borkent (1989) is a third instar of an undescribed species of *Contarinia* (broad sense). It has one pair of



Figs. 10–14. *Sitodiplosis mosellana*. 10, First instar (dorsal). 11, Same, detail of head and first two thoracic segments. 12, Same, detail of posterior segments. 13, Third instar, posterior part of eighth segment and terminal segment (dorsal). 14, Juxtaposed third instar (upper) and second instar (lower) terminal segments (dorsal). Bar lengths are in mm.

corniform (short and stout) papillae and three pairs of setiform papillae, two of which are of similar size. The presence of a spatula indicates that this specimen is also a third instar. Specimens in the USNM of similar larvae found in association with the wheat midge also have a spatula and are definitely third instars. These are also temporarily curated with wheat midge larvae until adults are found that can be identified further.

The third and fourth instars of Borkent (1989) are actually the second and third instar, respectively, of the wheat midge. Both are described in that paper as having a spatula, but the second instar has none. As noted above, older specimens of the second instar may appear to have a spatula due to the developing third instar inside (Figs. 8, 9). One can be certain of the train of instars of a particular species by observing nearly fully developed preecdysal instars within the body of a previous instar, as we have done here.

Borkent (1989) cited Borkent (in press), "Description of the larval instars of the Wheat Midge *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae). Can. J. Zool." No paper by Borkent on the subject of the wheat midge has appeared in the Canadian Journal of Zoology.

This occasion is taken to remove the name *Cecidomyia amyotii* Fitch from synonymy with the wheat midge. Felt (1925) listed *C. amyotii* as "probably a synonym of" the wheat midge and Foote (1965) cataloged it as a synonym of the wheat midge for the first time. According to Fitch's (1861) original description of *C. amyotii*, based on three specimens caught at a light, the female antenna has "eighteen (?) joints, not separated by pedicels, the joints globular." The female of the wheat midge has 12 antennal flagellomeres, each separated by a conspicuous pedicel or neck, so *C. amyotii* cannot be the wheat midge. Because the types of *C. amyotii* are presumably lost and the species cannot be determined with certainty, we consider this species a dubious name.

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THE LARVA OF *PELECINUS POLYTURATOR* (DRURY) (HYMENOPTERA: PELECINIDAE)

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Abstract.—The first instar larva and exuviae of the last instar larva of *Pelecinus polyturator* (Drury) are described, illustrated, and compared with published descriptions of other larvae of Proctotrupoidea.

Key Words: larval morphology, Pelecinidae, Proctotrupoidea

The application of characters from larval morphology to the study of relationships within the Hymenoptera is very uneven. There are some good examples of the usefulness of immatures as an additional source of data (e.g., Evans 1987), but for many superfamilies little or nothing is known. Progress in this area is hindered for several reasons. Most Apocrita are parasitoids of other insects, and the hosts for a number of groups are very poorly known. Many species are internal parasitoids; thus it is difficult to obtain early instars and often the larvae are highly simplified in structure.

Within the Hymenoptera a remarkable array of larval body plans is found. Clausen (1940) outlined fourteen types among the parasitic Hymenoptera alone. Some of these are highly simplified, "embryonic," forms, while others possess well-developed, exaggerated mandibles and caudal appendages. Later instars usually converge upon a generalized, hymenopteriform type. Little phylogenetic pattern has been found amidst this variety; at present we are confronted with a diversity of forms without any underlying organizing principle.

The superfamily Proctotrupoidea s. str. is comprised of ten extant families of internal parasitoids. The hosts for three of these (Renyxidae, Austroniidae, and Peradeniidae) are unknown, and only a bare minimum of information is available for the Monomachidae and Roproniidae. The only families for which immature stages have been described are the Diapriidae (a large group of nearly 2,000 recognized species), Proctotrupidae (331 described species), and Heloridae (a relict group of 10 extant species). In total, the larvae of only six species from this complex have been described. We report here on the larvae of another family, the Pelecinidae, a small group (only one species currently recognized) of uncertain affinities (Rasnitsyn 1980, Dowton et al. 1997).

MATERIALS AND METHODS

Five parasitoid larvae were dissected from larvae of Scarabaeidae (Coleoptera), and preserved in ethanol. The specimens

were found in the posterior two-thirds of the abdomen of the host. Three final instar exuviae were found attached to scarab remains from which *Pelecinus* had pupated. Specimens are stored in the collections of JBJ; the Ohio State University; the Insect Research Collection, University of Wisconsin; and El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas. Illustrations were made using a camera lucida of whole specimens under alcohol and exuviae in temporary slide mounts in glycerine jelly.

Pelecinus polyturator (Drury)

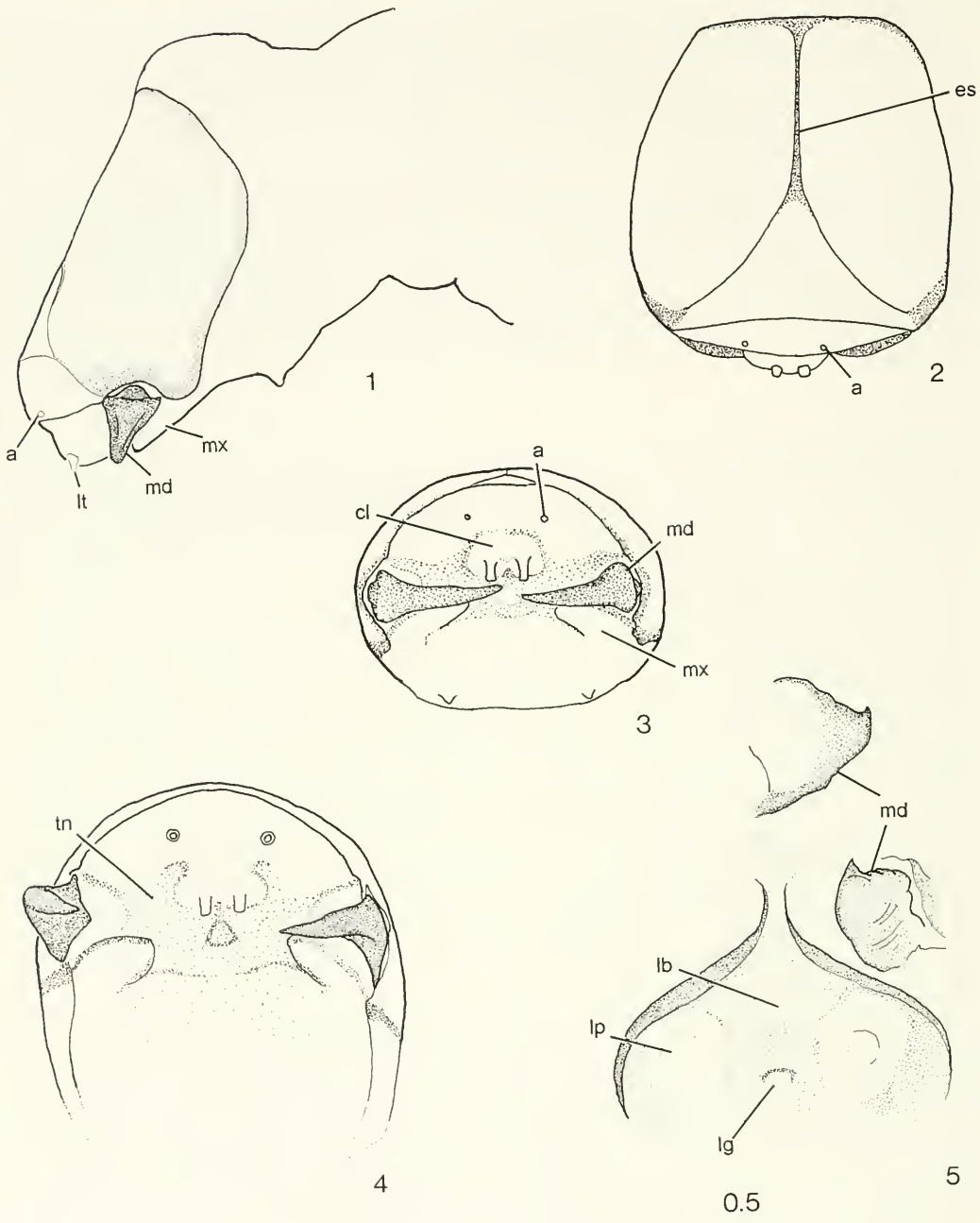
Material examined.—USA. Michigan, Newaygo Co., 18 April 1974, host in soil of oak forest, ex *Phyllophaga*, one first instar; Branch Co., 23 May 1974, hosts in soil of oak-hickory forest, four first instars, three from large 5 cm long larvae, probably *Phyllophaga*, one from small 2.5 cm larva, possibly *Serica* sp. Wisconsin, Marquette Co., 11 August 1992, in sandy soil of forest meadow, ex larva of *Phyllophaga drakei* (Kirby) one final instar exuviae; Jackson Co., 4 June 1992, ex *P. drakei*, one final instar exuviae; Oconto Co., 28 May 1996, ex *Phyllophaga rugosa* (Melsheimer), one final instar exuviae. MEXICO. Chiapas, Tenejapa, Balun Canal, 2,300 m, 14 February 1997, ex *Phyllophaga obsoleta* (Blanchard) third instar, one final instar exuviae.

First instar (Figs. 1–4).— Length 3.3–5.3 mm; mandibulate larva (Clausen 1940); head capsule well-developed, covering dorsal and lateral sides of head, margins darkly pigmented, sclerotization extending beyond margins, gradually disappearing posteriorly; epicranial suture (Fig. 2, *es*) well-developed; no indication of eyes; antenna (Figs. 1–3, *a*) indicated by small paired submedial papilla; clypeolabral area (Fig. 3, *cl*) largely membranous, supported by ovoid sclerotized ring, dorsal portion of this ring sometimes incomplete; labrum with two medial tubercles (Fig. 1, *lt*); mandible (Figs. 1, 3, *md*) strongly developed, falcate, bearing a small subapical tooth; maxilla (Fig. 1, 3, *mx*) supported anteriorly by narrow stipital sclerite, otherwise lobelike, membranous; maxillary palp, labium, and labial palp undifferentiated; head supported internally by extensive, strongly pigmented tentorium (Fig. 4, *tn*) in shape of central plate with anterior extensions continuous with labral sclerite, lateral arms surrounding base of mandibles, and broad posterior bilobed plate in labial region, a central ovoid foramen visible, anterior to this with more strongly pigmented triangular prominence, anterior apex of triangle produced into small costa extending into labrum; no prolegs visible; body with indeterminate number of segments, without setae, apex of abdomen acute; no spiracles visible.

Final instar (Fig. 5).—Head capsule with posterior sclerotized, pigmented band, otherwise largely membranous; mandible (*md*) very small, weakly articulated with head; antenna, labrum, maxilla, maxillary palp indistinguishable; labium (*lb*) visible as medial triangular raised surface behind mandibles, with large circular field corresponding to each labial palp (*lp*), a small central area presumably representing opening of labial gland (*lg*) between palpi; mouthparts unsupported by sclerotized pleurostoma or hypostoma; body with 7 pairs of spiracles visible; tracheae well-developed.

Discussion

The exuviae of the last instar larvae are associated with pharate adult *Pelecinus polyturator*, and their identity is unequivocal. The early instar larvae, however, are strikingly divergent in structure from the exuviae. Our determination of them was based on the fact that they were internal parasitoids dissected from larvae of *Phyllophaga* Harris (Coleoptera: Scarabaeidae), the only recorded host in the United States and Canada. The specimens also were collected in an area in which *Pelecinus* was very abundant. Muesebeck (1979) recorded *Tiphia berbereti* Allen, *T. tegulina* Malloch, *T. transversa* Say, *T. vulgaris* Robertson, and *T. intermedia* Malloch (Tiphiidae); *Myzin-*



Figs. 1–5. *Pelecinus polyturator*, larva. 1–4, Head of first instar. 1, Lateral view. 2, Dorsal view. 3, Frontal view, specimen with mandibles closed. 4, Frontal view, specimen with open mandibles exposing tentorium. 5, Mouthparts from final instar exuviae, right mandible detached. Abbreviations: a = antenna; cl = clypeolabral area; es = epicranial suture; lb = labium; lg = opening of labial gland; lp = labial palp; lt = labral tubercle; md = mandible; mx = maxilla; tn = tentorium. Scale in mm.

um quinquecinctum (Fabricius) (Tiphiidae); and *Ophion nigrovarius* Provancher (Ichneumonidae) as parasitoids of *Phyllophaga*. Woodruff and Beck (1989) listed a second species of *Ophion* as well as a number of additional species of tiphiids and scoliids. We ruled out the aculeates because they are external parasitoids. Ichneumonoids usually are characterized by the possession of a hypostomal spur (Short 1978), a structure that was not observed in these specimens.

Determination of the number of larval instars of internal parasitoids requires large numbers of observations of cohorts of known age in order to detect structural changes associated with molting. This has not been done yet for any species of proctotrupoid, and no one has yet been able to rear *Pelecinus* through its life cycle. We could not determine the age of the observed larvae directly or infer their age from published observations of related species. Clausen (1940) stated that the characteristics that set apart mandibulate larvae are lost at the first molt. This was confirmed by Clancy (1946) in his studies of *Helorus*, another proctotrupoid. Therefore, we concluded that the larvae dissected from the hosts must be late first instars.

Very little information on the immature stages of proctotrupoids exists to form a context in which to discuss the structural features of *Pelecinus*. Larvae have been described and illustrated for *Helorus anomalipes* (Panzer) (Heloridae; Clancy 1946), an unidentified species of *Basalys* Westwood (Diapriidae; Simmonds 1952), *Basalys tritoma* Thomson (Diapriidae; Wright et al. 1946), *Coptera silvestrii* (Kieffer) (Diapriidae; Pemberton and Willard 1918), *Paracodrus apterogynus* (Haliday) (Proctotrupidae; Zolk 1924), *Phaenoserphus viator* (Haliday) (Proctotrupidae; Eastham 1929), and *Brachyserphus parvulus* (Nees ab Esenbeck) (Proctotrupidae; Osborne 1960). Large, sickle-shaped mandibles have been reported in the first instar for all these species. A sclerotized head capsule was described in *H. anomalipes*, *B. tritoma*, and *C. silvestril. Phaenoserphus viator* lacks a complete head capsule, but does have a sclerotized ring surrounding the mouthparts. Distinct antennal lobes are found in the helorid, *Basalys* spp. and the proctotrupids, larger and more prominent than the structures found in *Pelecinus*. We observed no prolegs on any of the first instar larvae; these structures have been reported for *H. anomalipes*, *P. viator*, *B. parvulus*, and an unidentified proctotrupid (Clausen 1940; presumably *Nothoserphus scymni* Ashmead). Two of our specimens have paired, nipple-like protuberances beneath the posterior portion of the head capsule (visible in Fig. 1). Because of their position, we hesitate to call these prolegs or to homologize them with the labial palpi. The number of observed spiracles reported varies from three (*B. tritoma*, *C. silvestrii*) to ten pairs (*P. viator*).

The most striking feature we observed in the first-instar larva was the large tentorial endoskeleton. A similar structure was very briefly described in *P. viator* by Eastham (1929), suggesting that it may not have been as apparent or strongly pigmented as in *Pelecinus*. The tentorium is not mentioned in the other descriptions.

The larval specimens were dissected from hosts in the spring (18 April, 1974; 23 May, 1974) in Michigan. Therefore, it appears that the species overwinters as late first instars within the *Phyllophaga* larvae. No more than a single larva was found in any one host. Three specimens were recovered from large (5 cm) hosts, presumably the final instar of the beetle. A fourth was found in a much smaller larva, either a much younger specimen or a different genus, perhaps *Serica* MacLeay (Coleoptera: Scarabaeidae). Host size may contribute to the large variation in size of adult *Pelecinus*.

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NEW GENUS AND NEW SPECIES OF AMORBINI (HETEROPTERA: COREIDAE) FROM AUSTRALIA

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Abstract.—***Kormijirania,* n. gen.,** and two **new species, *K. magna*** and ***K. parva,*** collected in Eastern Australia are described in the tribe Amorbini (Coreidae). Habitus illustrations, drawings of the male and female genitalia, and a key are provided.

Key Words: Insecta, Heteroptera, Coreidae, Amorbini, new genus, new species, Eastern Australia

The tribe Amorbini (Hemiptera: Heteroptera: Coreidae) is represented by 7 genera in the Australian region: *Acroelytron* Mayr (1 species), *Amorbus* Dallas (15 species), *Cneius* Stål (1 species), *Gelonus* Stål (1 species), *Kurnaina* Distant (1 species), *Tambourina* Distant (1 species), and a new genus (2 species) (Brailovsky and Monteith, in press).

The present paper adds one new genus and two new species of Amorbini from eastern Australia. For several years, the species discussed here have remained unnamed and undescribed in the hope that additional specimens would be found. However, it seems desirable to draw the attention of entomologists to these species in the hope that additional specimens will be collected and some information obtained on their ecology and food requirements. Two striking features of this new genus are the upturned juga forming a stout long horn or conical tubercle, and the mandibular plate expanded on a remarkable stout conical tubercle.

The following abbreviations are used for the institutions cited in this paper: BPBM (Bernice P. Bishop Museum, Honolulu, Hawaii); SAMA (South Australian Museum, Adelaide); UNAM (Instituto de Biología, Universidad Nacional Autónoma de México).

All measurements are given in millimeters.

Kormijirania Brailovsky and Cassis, new genus

Diagnosis.—This new genus resembles *Gelonus* Stål (1865) in having the head wider than long, tylus unarmed and extending anteriorly to the juga, antenniferous tubercles unarmed, tibiae sulcate, not foliate, and abdominal sternite VII of the female with plica and fissura. It is easily distinguished because it is the only known genus in the tribe Amorbini with the upturned juga forming a stout long horn or conical tubercle, and the mandibular plate strikingly expanded on a large conical tubercle.

Kormijirania has a stout antennal segment I, short, and barely crested, antennal segments II and III almost cylindrical, barely flattened, buccula anteriorly with a clear spine-like projection, pronotum slightly wider than long, and fore and middle femora ventrally with small granules or tiny spine-like projections, never with a large and laminate subdistal spine. In *Gelonus* the

juga are flattened, the mandibular plate unarmed, antennal segments I to III uniformly cylindrical, not crested or flattened, buccula anteriorly rounded, pronotum clearly wider than long, and fore and middle femora ventrally provided with a large and unique subdistal laminate spine.

A new genus (Brailovsky and Monteith, in press), is related to *Gelonus* and *Kormijirania* and is recognized by the laterally compressed tylus, which is projected upward as an acute projection, with femora unarmed, juga flat, mandibular plate unarmed, and antennal segments I to III cylindrical.

Description.—Macropterous, body stout, moderate sized. *Head:* Width across eyes greater than length, quadrate, dorsally flat, non declivent, barely produced beyond antenniferous tubercles, with deep circular pit close to base of tylus; tylus unarmed, slightly deflexed; juga shorter than tylus, upturned to form a stout long horn or conical tubercle; antenniferous tubercle unarmed, prominently produced, wide, separated by distance greater than their own width; sides of head in front of eyes almost straight; antennal segment I robust, thickest, barely crested, constricted basally; segments II and III stout, cylindrical, barely flattened; segment IV fusiform; antennal segment II longest, IV shortest, and III longer than I; ocelli conspicuous, closer to eyes, and located on an hypothetical line with lower margin slightly above lower margin of eyes; preocellar pit deep; eyes protruding; postocular tubercle markedly produced; buccula rounded, short, not projecting beyond anterior third of antenniferous tubercles, slightly raised, anteriorly with a sharp spine-like projection, and posteriorly closed; rostrum reaching posterior third of mesosternum or anterior third of metasternum; rostral segment III shortest, I longest, and II longer than IV; mandibular plate expanded on a strong conical tubercle or acute tooth; ventrally with a deep longitudinal groove along midline to receive first and anterior third of rostral segment II; mandibular plate with markedly stout conical tubercle.

Thorax: Pronotum wider than long, trapeziform, non declivent; collar wide; frontal angles produced forward as rounded teeth; humeral angles rounded, not exposed; anterolateral margins slightly emarginate, obliquely straight, finely serrate; posterolateral margins sinuate, entire; posterior border concave, entire; callar region indistinct, transversely flat, separated along midline by an obscure longitudinal groove; posterior lobe with transverse ridge, distinctly raised; prosternum mesally with a slight depression; mesosternum with deep longitudinal groove to receive rostrum; anterior third of mesosternum without lateral expansions; anterior lobe of metathoracic peritreme elevated, irregularly reniform, posterior lobe sharp, small.

Legs: Short; femora slightly incrassate; fore and middle femora densely granulate, with small spine-like projections both dorsally and ventrally; hind femur slightly granulate, ventrally armed with two short subdistal spines or very tiny tubercles; tibiae terete, sulcate.

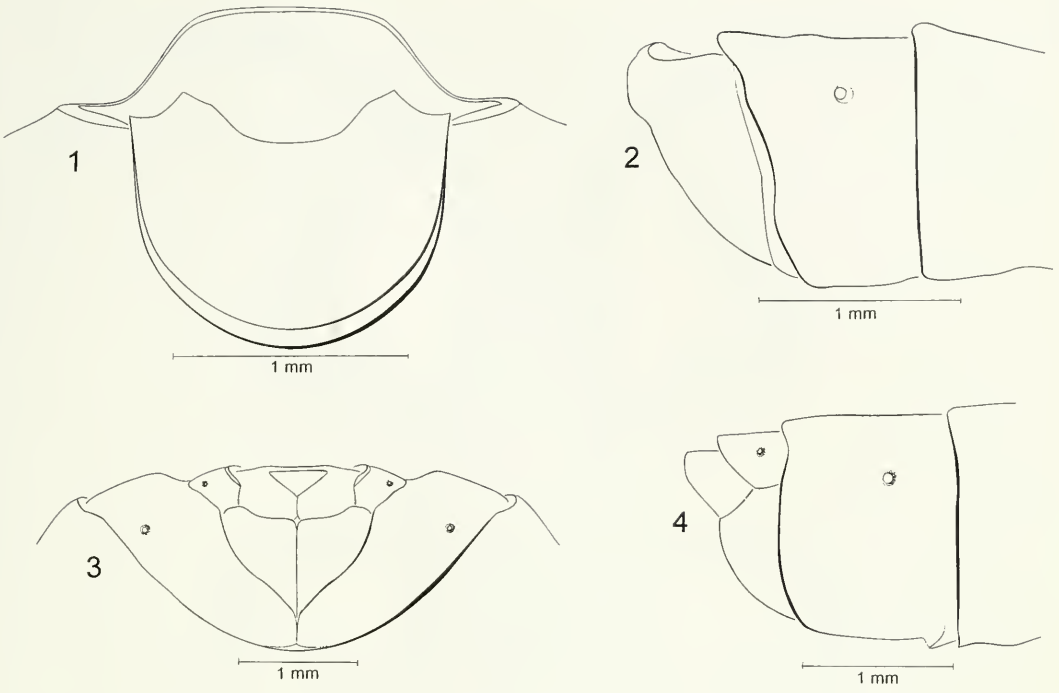
Scutellum: Triangular, longer than wide; apex truncated or subacute; disc flat.

Hemelytra: Macropterous, almost reaching apex of last abdominal segment; costal margin emarginate; apical margin straight; apical angle short, barely reaching middle third of hemelytral membrane.

Abdomen: Connexival segments reflexed above margin of hemelytron at rest; upper margin weakly serrate; posterior angles of connexival segments simple, not spinose; abdominal spiracles II to VII submarginal, closer to middle third.

Male genitalia: Genital capsule: Simple; posteroventral border slightly concave, with posterolateral angles broadly produced (Figs. 1, 2).

Female genitalia: Abdominal sternite VII with plica and fissura; plica triangular, slightly elevated, apically subacute, and reaching anterior third of sternite VII.



Figs. 1–4. 1, 2. Male genital capsule of *Kormijirania parva*. 1, Caudal view. 2, Lateral view. 3, 4, Female genital plates of *K. magna*. 3, Caudal view. 4, Lateral view.

Genital segments: Gonocoxae I enlarged dorso-ventrally, in caudal view closed, in lateral view slightly convex, with upper margin sinuate; paratergite VIII triangular, with spiracle visible; paratergite IX square, larger than paratergite VIII (Figs. 3, 4).

Integument: Body surface rather dull, almost glabrous. Head, antennal segments I to III, pronotum, clavus, corium, legs, connexival segments, propleuron, mesopleuron, metapleuron, and pleural abdominal sterna densely granulate; prosternum, mesosternum, metasternum, abdominal sterna, and genital plates almost smooth; posterior lobe of pronotum, clavus and corium, densely punctate.

Etymology.—We are pleased to name this new genus for Dr. Nicholas A. Kormilev, distinguished hemipterist.

Type species.—*Kormijirania parva* Brailovsky and Cassis, new species.

Kormijirania magna Brailovsky and Cassis, new species

(Figs. 3–5)

Description.—Measurements: *Female:* Head length 1.39; width across eyes 2.04; interocular space 1.30; interocellar space 0.46; preocular distance 1.05; length of antennal segments: I, 1.79; II, 2.13; III and IV mutilated. Pronotum: Total length 2.54, width across frontal angles 1.89; width across humeral angles 2.97. Scutellar length 1.51; width 1.24. Total body length 12.10.

Female: Dorsal coloration: Head, antennal segments I and II (III and IV mutilated), anterior lobe of pronotal disk, clavus and corium dirty yellow with red-brown to chestnut-orange punctures and tubercles; posterior lobe of pronotal disc dirty yellow with black to red-brown punctures; scutellum dark brown to black; apical angle of corium almost black; hemelytral membrane dirty white, with veins, basal angle, and

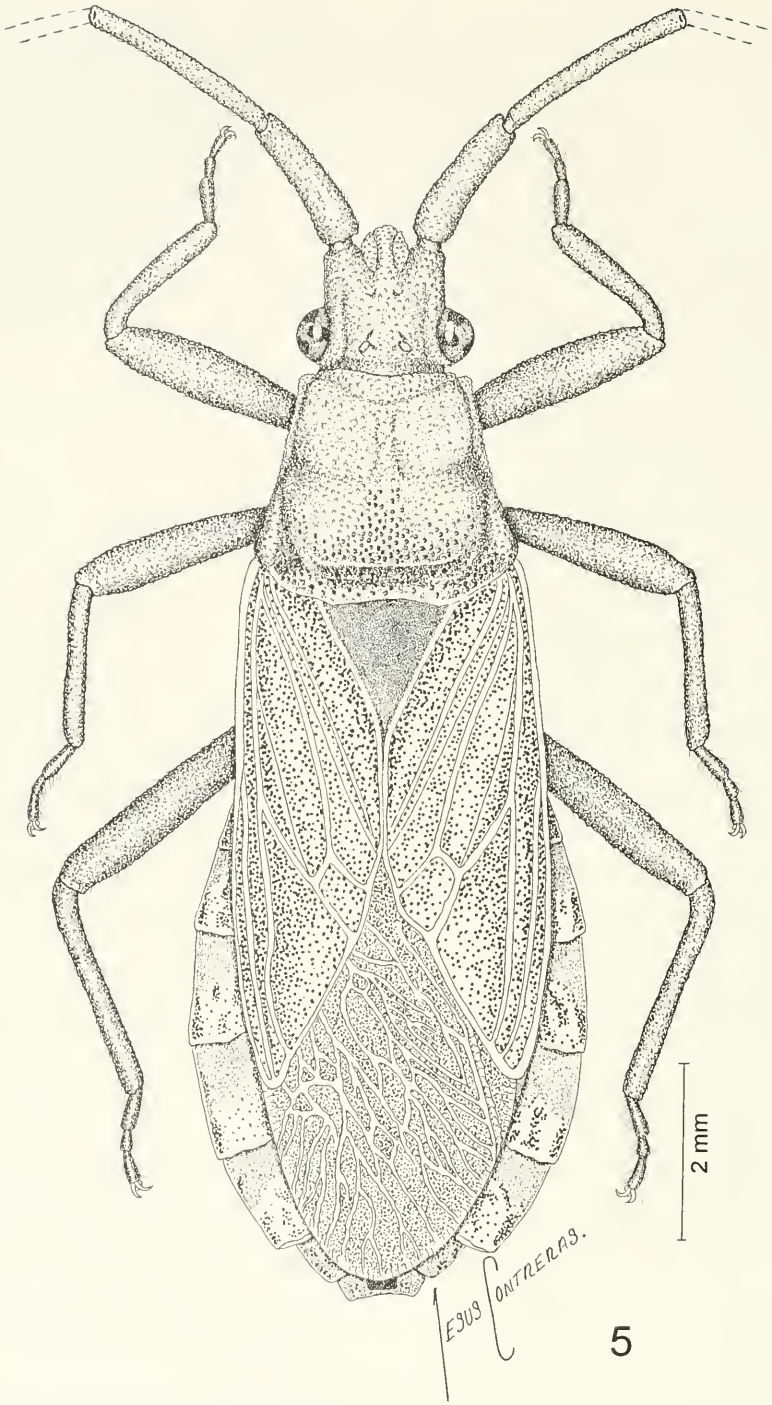


Fig. 5. Dorsal view of *Kormijirania magna* (♀).

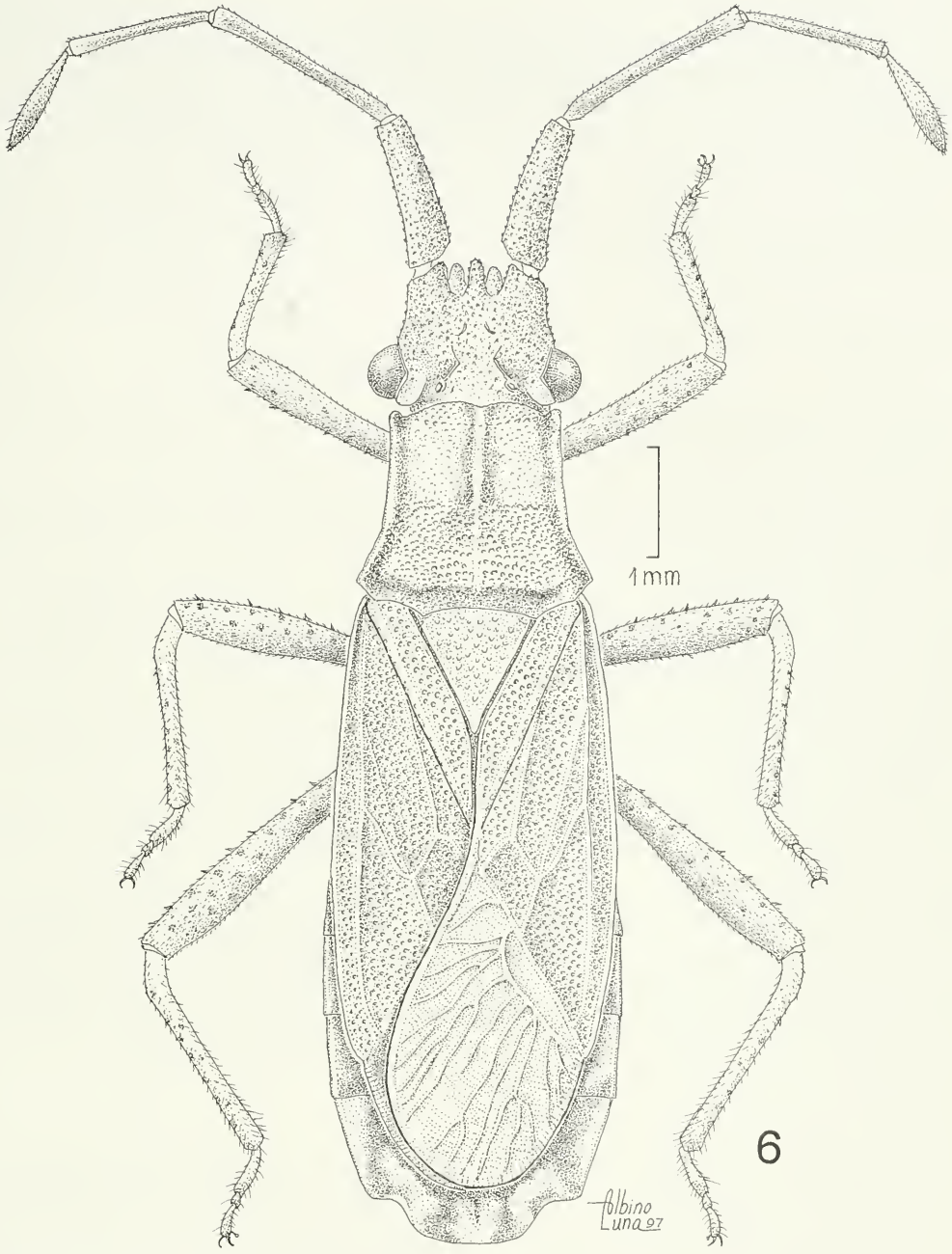


Fig. 6. Dorsal view of *Kormijirania parva* (♂).

scattered spots pale brown; connexival segments III to VIII light orange yellow, with upper margin of posterior third, and tubercles brown; connexival segment IX pale orange yellow, with black quadrate spot on middle third. Ventral coloration: Including rostral segments I to IV (apex of IV black), and legs dirty yellow with red-brown tubercles; abdominal sterna, and genital plates shiny yellow, with pale orange discoidal spots. *Structure:* Genital plates as in Figs. 3, 4.

Male: Unknown

Type material.—Holotype: ♀, Australia, Queensland, Mackay (without additional data) (BPBM).

Etymology.—Named for its large size; from the Latin word *magnus.*

Kormijirania parva Brailovsky and Cassis, new species

(Figs. 1, 2, 6)

Description.—Measurements: *Male:* Head length 1.20; width across eyes 1.86; interocular space 1.17; interocellar space 0.43; preocular distance 0.96; length of antennal segments: I, 1.24; II, 1.76; III, 1.39; IV, 1.14. Pronotum: Total length 1.70; width across frontal angles 1.51; width across humeral angles 1.96. Scutellar length 0.98; width 0.80. Total body length 9.00. *Female:* Head length 1.35; width across eyes 1.92; interocular space 1.20; interocellar space 0.43; preocular distance 0.96; length of antennal segments: I, 1.36; II, 1.87; III, 1.54; IV, mutilated. Pronotum: Total length 2.10; width across frontal angles 1.70; width across humeral angles 2.25. Scutellar length 1.24; width 1.02. Total body length 10.00.

Male: Dorsal coloration: Yellow with punctures orange hazel; ocellar tubercle red brown; antennal segments I to III yellow with red brown tubercles; segment IV with anterior half whitish yellow, and posterior half orange hazel; humeral angles red brown; apex of scutellum whitish yellow; hemelytral membrane dirty white, with veins, basal angle, and scattered spots pale brown; connexival segments II to VII yellow with upper margin of posterior third or entirely the posterior third reddish brown; abdominal segments I to VI light orange yellow and VII yellow with H-shaped dark spot. *Ventral coloration:* Included rostral segments I to IV (apex of IV black), buccula, and anterior and posterior lobe of metathoracic peritreme light yellow with some red-brown tubercles; genital capsule dark brown with three irregular yellow spots; legs yellow with red to pink tubercles. Structure: Genital capsule as in Figs. 1–2.

Female: Similar to male.

Type material.—*Holotype:* ♂, Australia, Cairns District, Col. A. M. Lea (without additional data) (SAMA). *Paratype:* 1 ♀, same data as holotype (SAMA). Both specimens glued on the same card.

Etymology.—Named for its small size; from the Latin word *parva,* rather small.

Key to Species of *Kormijirania*

1. Femora dirty yellow without red to pink tubercles (Fig. 5); antennal segment I longer than 1.70, and II longer than 2.00 . . . . . *magna* Brailovsky and Cassis, new species
– Femora yellow with red to pink tubercles (Fig. 6); antennal segment I shorter than 1.40, and II shorter than 1.90 . . . . . *parva* Brailovsky and Cassis, new species

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA ARIZONENSIS* MALLOCH (DIPTERA: TEPHRITIDAE) ON *TRIXIS CALIFORNICA* KELLOGG VAR. *CALIFORNICA* (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea arizonensis* Malloch is a monophagous, univoltine fruit fly (Diptera: Tephritidae) infesting flower heads of *Trixis californica* Kellogg var. *californica* (Asteraceae) in southern California. The egg, first- and third-instar larvae, and puparia are described and figured for the first time. As with each of the eight other *Trupanea* species previously studied, the lateral spiracular complex of the third instar is unique to *T. arizonensis*, comprising three verruciform sensilla on the meso- and metathorax and two verruciform sensilla on each abdominal segment. The third instar of *T. arizonensis* also differs from those of other *Trupanea* species previously studied in that both the meso- and metathorax are circumscribed by verruciform sensilla. The life cycle is of the aggregative type; whereby, the adults are long-lived and comprise the over-summering and over-wintering stage that returns with winter rainfall to aggregate on regrowing host plants for mating, and for oviposition during spring in the preblossom flower heads. The first instar tunneled into a single floral tube or ovule of a single immature floret, and each second and third instar continued its development by feeding principally on sap conducted to the excavated distal end of the same, then slightly stunted ovule. Pupariation occurs in the open flower heads, within which an average of 13% of the achenes were destroyed among heads containing puparia. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from individual puparia of *T. arizonensis* as a solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Trupanea*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, host-plant range, parasitoid

Trupanea arizonensis Malloch (Diptera: Tephritidae) is a rarely collected, monophagous or nearly monophagous species belonging to one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California (Foote and Blanc 1963, Foote et al. 1993). But, being of little or no economic importance, most species of *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until detailed life histories were published for nine species from southern California (Cavender and Goeden 1982; Goeden 1987, 1988; Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of the immature stages of eight of these species (Cavender and Goeden 1982, Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998). This paper describes the life history and

most immature stages of a tenth species, *T. arizonensis*.

Materials and Methods

This study was based in large part on dissections of subsamples of flower heads of *Trixis californica* Kellogg var. *californica* (Asteraceae) infested by *T. arizonensis* from samples collected during 1991–1995 in the low-elevation Colorado (northern Sonoran) Desert and high-elevation, eastern Mojave Desert in southern California in the manner described by Goeden (1985, 1992). The principal study sites in the Colorado Desert were Valliceto Valley at the mouth of Smugglers Canyon, 440-m elevation, San Diego Co.; the Edmund C. Jaeger Nature Preserve at 847 m, Desert Center, Riverside Co.; and Chino Canyon, 1 km NW of Palm Springs, at 270 m, Riverside Co. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in coldchests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Nine eggs, 18 first- and 16 third-instar larvae, and six puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996a), Goeden and Teerink (1997, 1998), Goeden et al. (1998a, b), and Teerink and Goeden (1998), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. arizonensis* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and now maintained by RDG.

Results and Discussion

Taxonomy

Adult.—*Trupanea arizonensis* was first described by Malloch (1942) as *Trypanea arizonensis*. Malloch (1942), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern, which Foote (1960) described as not sexually dimorphic, but essentially alike in every important character in the female and male. However, the variable nature of this wing pattern, especially among males, initially caused Goeden and Ricker (1989) to misidentify specimens reared from *Trixis californica* as *Trupanea actinobola* (Loew), another variable species (Foote and Blanc 1963, Foote et al. 1993, Goeden et al. 1998b). Goeden (1992) corrected this error and re-identified the flies from *T. californica* as *T. arizonensis*; moreover, Goeden et al. (1998b) further supported this identification based on the different tribal- and separate, subtribal-level, host-plant affiliations

of the three biotypes of *T. actinobola* in southern California, which exclude *Trixis californica* in the tribe Mutisieae (see below).

Nine (10.6%) of 85 ♂, but none of 65 ♀ of *Trupanea arizonensis* in the research collection of RDG reared from flower heads of *Trixis californica* have only one dark ray, not two rays, contrary to Foote et al. (1993), extending into cell dm from vein CuA_1. Moreover, the single, remaining, what is otherwise called the distal ray (Foote et al. 1993), is broken in cell dm and does not reach vein CuA_1 in 39 ♂ (45.9%) and 18 ♀ (27.7%). There is no dark spot on vein CuA_1 or on the wing margin in line with the broken distal ray in an additional 10 ♂ (11.8%) and 3 ♀ (4.6%), or with such a dark spot on CuA_1 or on the wing margin in line with the broken distal ray in an additional 2 ♂ (2.4%) and 3 ♀ (4.6%), respectively. The proximal ray usually extends, though sometimes very limitedly, into cell dm in 76 ♂ (89%) and all 65 ♀, and there is usually (not always, Foote et al. 1993) a dark spot on vein CuA_1 in line with it; however, in 3 ♀ (4.6%) the broken proximal ray is reduced to a spot in the middle of cell dm in line with a spot on vein CuA_1, and another 2 ♂ (2.3%) and 1 ♀ (1.5%) lack a dark spot in line with it. Therefore, all females and most males of *T. arizonensis* can still be distinguished from other *Trupanea* spp. by use of the separate keys for the two sexes in Foote et al. (1993) if one is aware of the above variations and perceives two dark rays, however abbreviated, extending into cell dm, neither of which necessarily crosses vein CuA_1, much less continues to the hind wing margin. Males with only one dark ray extending into cell dm from vein CuA_1, like the nine noted above, will run to *T. actinobola*, as they did earlier for Goeden and Ricker (1989). Couplet 8 (pp. 421 and 424 in Foote et al. 1993) distinguishing *T. maculigera* Foote from *T. arizonensis* apparently remains valid; although the angles formed by the proximal and distal rays, not the distances between them along vein CuA_1, should be compared with specimens of *T. arizonensis* having proximal or distal rays or both broken in cell dm.

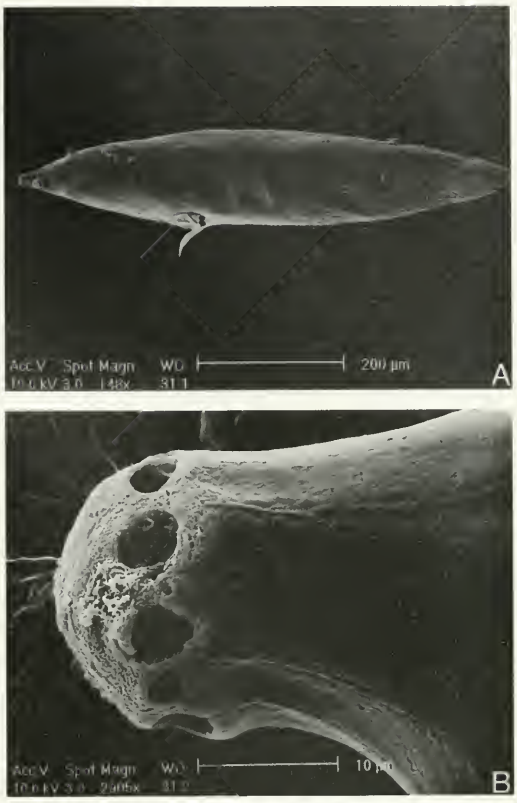

Fig. 1. Egg of *Trupanea arizonensis:* (A) habitus, pedicel to left; (B) pedicel.

Immature stages.—The immature stages of *T. arizonensis* heretofore have neither been described nor illustrated.

Egg: Seventy eggs of *T. arizonensis* dissected from heads of *T. californica* were white, opaque, smooth; elongate-ellipsoidal, 0.70 ± 0.006 (range, 0.54–0.85) mm long, 0.15 ± 0.002 (range, 0.12–0.23) mm wide, smoothly rounded at tapered basal end (Fig. 1A), pedicel 0.02 mm long, with single row of subcircular aeropyles (Fig. 1B).

The egg of *T. arizonensis* is narrow like the eggs of *T. actinobola* (Goeden et al. 1998b) and *T. pseudovicina* (Goeden and Teerink 1998), but is much longer than both of these species. The egg body in *T. ari-*

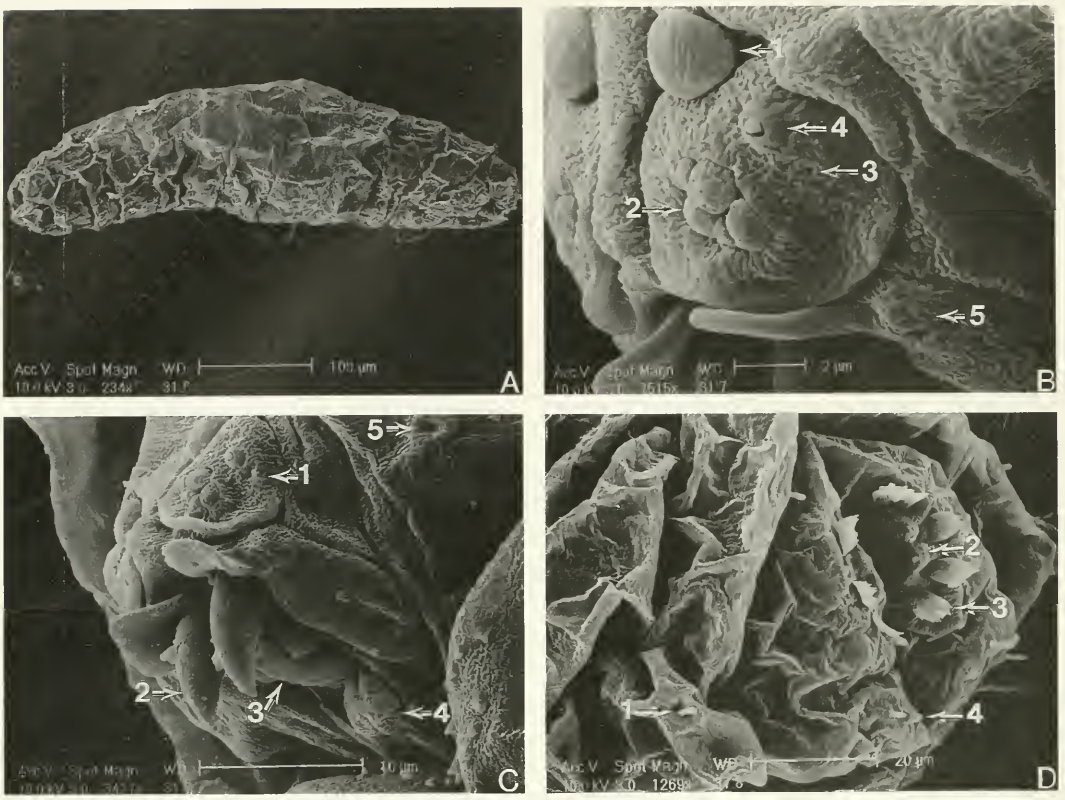

Fig. 2. First instar of *Trupanea arizonensis:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1, dorsal sensory organ, 2, terminal sensory organ, 3, pit sensory organ, 4, lateral sensory organ, 5, stomal sense organ; (C) gnathocephalon, ventral view, 1, anterior sensory lobe, 2, mouth hook, 3, median oral lobe, 4, labial lobe, 5, pit sensillum; (D) caudal segment, 1, stelex sensillum, 2, rima, 3, interspiracular process, 4, intermediate sensory complex.

zonensis tapers smoothly into the pedicel, more so than in the other *Trupanea* species previously studied (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998). The pedicel is similar to these other congeners in having a single row of aeropyles (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Teerink and Goeden 1998), with the exception of *T. bisetosa* (Coquillett), which has one or two rows (Knio et al. 1996a).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines (Fig. 2A); gnathocephalon smooth (roughness in Fig. 2 is an artifact), lacking rugose pads (Fig. 2C); dorsal sensory organ a dome-shaped papilla (Fig. 2B-1); anterior sensory lobe (Fig. 2C-1) bears terminal sensory organ (Fig. 2B-2), pit sensory organ (Fig. 2B-3), lateral sensory organ (Fig. 2B-4), and supralateral sensory organ; stomal sense organ indistinct (Fig. 2B-5); mouth hooks bidentate (Fig. 2C-2); median oral lobe laterally flattened (Fig. 2C-3), labial lobe (Fig. 2C-4) attached to median oral lobe; pit sensillum laterad of anterior sensory lobe (Fig. 2C-5); prothorax lacking rugose pads, few minute acanthae ventrad of mouth lumen; stelex sensilla circumscribe caudal segment in 2-dorsal, 4-ventral arrangement (Fig. 2D-1); posterior spiracular plates bear two ovoid rimae (Fig. 2D-2), and four, spatulate interspiracular processes (Fig. 2D-3); intermediate sensory

complex consists of a medusoid and stelex sensillum (Fig. 2D-4).

The first instar of *T. arizonensis* is very similar to other congeners previously studied in habitus and sensory structures (Goeden and Teerink 1998; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998). The lateral spiracular complex was not seen. There are slight differences in the interspiracular processes. In *T. jonesi*, the interspiracular processes are greatly reduced (Goeden et al. 1998a), in *T. arizonensis* and *T. conjuncta* the processes are single and spatulate (Teerink and Goeden 1998), and in *T. pseudovicina* Hering, *T. actinobola, T. bisetosa* and *T. nigricornis* (Coquillett), the interspiracular processes are divided, each with 1–4 branches (Goeden and Teerink 1997; Goeden et al. 1998b; Knio et al. 1996a).

Third instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines in bands increasing in width posteriorly (Fig. 3A); gnathocephalon conical, rugose pads dorsal and lateral to mouth lumen (Fig. 3B-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-1); anterior sensory lobe (Fig. 3B-3) bears the terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-4, 3C-6); mouth hooks tridentate (Fig. 3B-5, 3D-1); median oral lobe tapered anteriorly (Fig. 3D-2); six pit sensilla circumscribe gnathocephalon posterior to rugose pads (Fig. 3B-6); minute acanthae circumscribe anterior margin of prothorax (Fig. 3E-1); rugose pads (Fig. 3E-2) and a single row of verruciform sensilla (Fig. 3E-3) circumscribe prothorax posteriorad of minute acanthae; additional verruciform sensilla on dorsal half of prothorax (Fig. 3E-4); anterior thoracic spiracle on posterior margin of prothorax bears three ovoid papillae (Fig. 3E-5), meso- and metathorax circumscribed by verruciform sensilla; meso- and metathoracic lateral spiracular complexes consist of a spiracle (Fig. 3F-1), and three verruciform sensilla (Fig. 3F-2); abdominal lateral spiracular complex consists of a spiracle (Fig. 3G-1) and two verruciform sensilla (Fig. 3G-2); caudal segment circumscribed by minute acanthae (Fig. 3H-1); posterior spiracular plates bear three ovoid rimae, ca. 0.03 mm in length (Fig. 3H-2), and four interspiracular processes, each with 3–5 branches, longest measuring 0.02 mm (Fig. 3H-3); intermediate sensory complex consists of a stelex sensillum and a medusoid sensillum (not shown).

The third instar of *T. arizonensis* is similar in general habitus to *T. pseudovicina* in being elongate-cylindrical, maybe even more attenuated (Goeden and Teerink 1998). As with the third instars of each of the eight other *Trupanea* species previously studied, the lateral spiracular complex is unique to *T. arizonensis*, with three verruciform sensilla in the meso- and metathorax and two verruciform sensilla in the abdominal segments (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998). There are other differences between individual species. *Trupanea arizonensis* differs from *T. actinobola* in lacking elongated integumental petals; *T. arizonensis* has fewer rugose pads circumscribing the prothorax, and the prothorax is completely circumscribed by minute acanthae (Goeden et al. 1998b). Also, *T. arizonensis* differs from the other *Trupanea* species previously studied, in that the meso- and metathorax are circumscribed by verruciform sensilla; whereas, only the mesothorax in *T. nigricornis* was circumscribed by verruciform sensilla (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998). *Trupanea arizonensis* differs from its symphagous congener in *Trixis californica*, *T. conjuncta*, in not being finely punctate nor barrel-shaped, and *T. arizonensis* also has

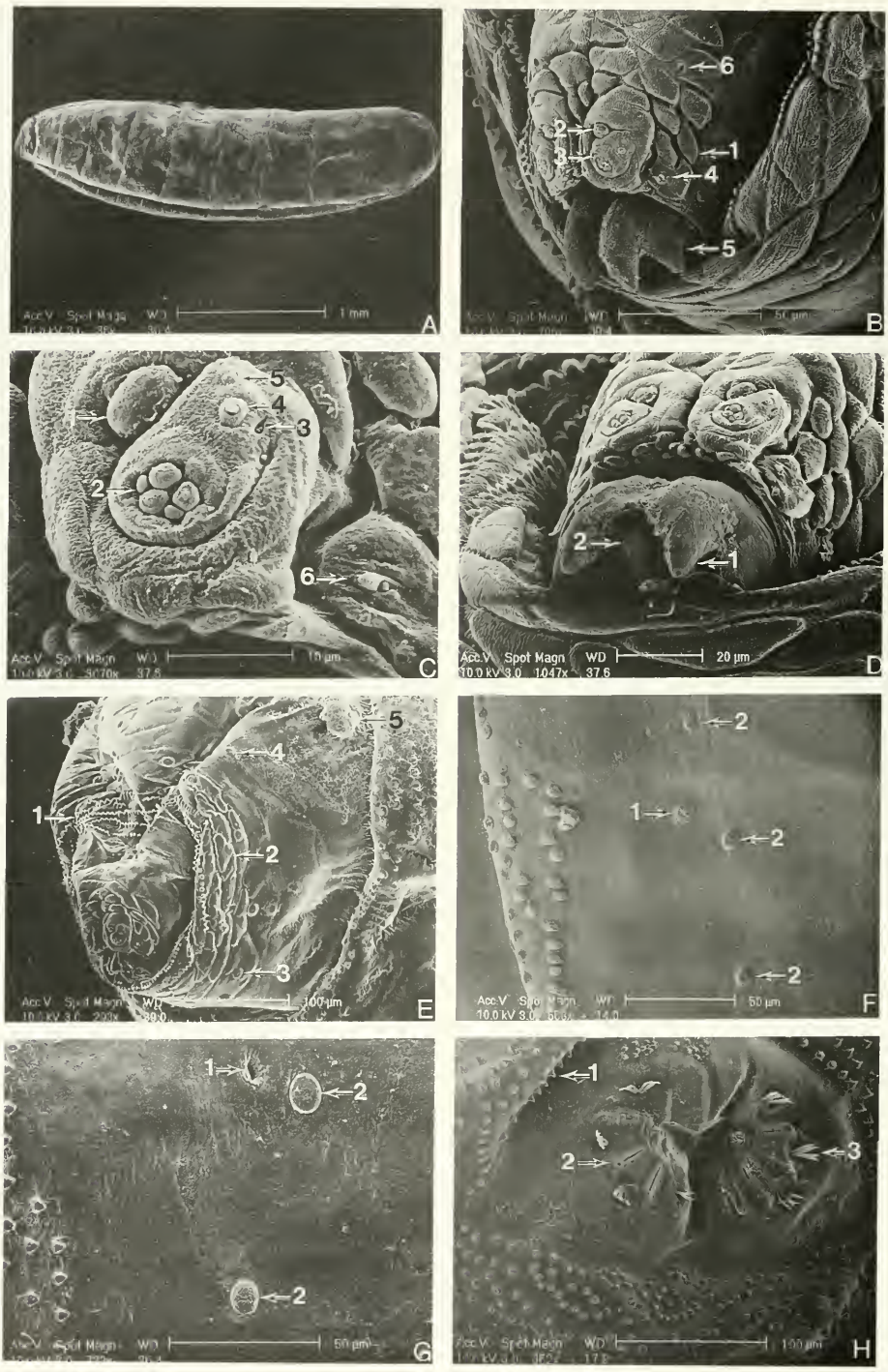

Fig. 3. Third instar of *Trupanea arizonensis:* (A) habitus, anterior end to left; (B) gnathocephalon, anterolateral view, 1, rugose pads, 2, dorsal sensory organ, 3, anterior sensory lobe, 4, stomal sense organ, 5, mouth hook, 6, pit sensillum; (C) anterior sensory lobe, 1, dorsal sensory organ, 2, terminal sensory organ, 3, pit sensory organ, 4, lateral sensory organ, 5, supralateral sensory organ, 6, stomal sense organ; (D) gnathocephalon, ventral view, 1, mouth hook, 2, median oral lobe; (E) gnathocephalon, prothorax, lateral view, 1, minute acanthae,

fewer papillae in the anterior thoracic spiracle (Teerink and Goeden 1998).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines, (Fig. 4A); anterior end bears the invagination scar (Fig. 4B-1), and anterior thoracic spiracles (Fig. 4B-2); caudal segment circumscribed by minute acanthae (Fig. 4C-1); posterior spiracular plates bear three ovoid rimae (Fig. 4C-2) and four interspiracular processes, each with 3–5 branches (Fig. 4C-3). Sixty-four puparia averaged 2.68 ± 0.02 (range, 2.28–3.24) mm in length; 0.92 ± 0.01 (range, 0.76–1.16) mm in width.

Distribution and Hosts

The distribution of *T. arizonensis* mapped in North America north of Mexico by Foote et al. (1993) is confined to several, mostly U.S. southern border locations in Arizona, California, and Texas.

Goeden and Ricker (1989) reported *T. arizonensis* as *T. actinobola* from *Trixis californica*, and as mentioned above, Goeden (1992) corrected this misidentification and thus provided the first and sole host-plant record for *T. arizonensis*. This host-plant belongs to the subtribe Nassauviinae in the tribe Mutisieae of the Asteraceae (Hickman 1993, Bremer 1994); this tribe rarely occurs in North America (Bremer 1994), and is represented by only three species in California (Munz 1974), the second of which, *Acourtia microcephala* de-Candolle, does not host *T. arizonensis* (Goeden and Headrick 1991). The third plant species is the rare, unsampled, xerophytic shrub, *Hecastocleis shockleyi* A. Gray (Hickman 1993, Bremer 1994). In comparison, *T. actinobola*, apparently is confined to three subtribes of the different tribe Astereae in California (Goeden and Teerink 1998b). Accordingly, *T. arizonensis* may be either a true monophage (one host-plant species) on *Trixis californica*, which occurs as far east as Texas in North America north of Mexico (Hickman 1993), or a near-monophage (one host-plant genus) on one or more of the 50 other congeners in the southwestern United States, Central, and South America and West Indies (Bremer 1994). Like several other tephritid species that we have studied, e.g., *Trupanea conjuncta* (Goeden 1987), *T. pseudovicina* Hering (Goeden and Teerink 1998), and *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991), *Trupanea arizonensis* represents a native southern California tephritid closely associated with a native host-plant, which is primarily distributed in Mexico and southward, where these tephritids remain little known.

Biology

Egg.—In 38 closed, preblossom, immature flower heads, all 130 eggs were inserted pedicel-last between the tips of the phyllaries, perpendicular to the receptacle, and among or within the florets and pappus (Fig. 5A). The diameters of the receptacles of 32 of these flower heads containing eggs averaged 2.6 ± 0.1 (range, 1.3–3.7) mm, and the 38 infested heads contained an average of 3.4 ± 0.3 (range, 1–9) eggs oviposited, mostly singly, or side-by-side in pairs (Figs. 5A, B), but also in groups of up to five, by one or more females.

Larva.—Upon eclosion, first instars tunneled into a single floral tube or ovule of an immature floret (Fig. 5C). An average of 2.1 ± 0.2 (range, 1–4) first instars was found feeding within 22 closed, preblossom flower heads. The receptacles of these heads averaged 3.1 ± 0.2 (range, 2.2–4.6) mm in diameter with an average of 18 ± 2

←

2, rugose pads, 3, verruciform sensillum, 4, verruciform sensillum, 5, anterior thoracic spiracle; (F) metathorax, 1, spiracle, 2, verruciform sensilla; (G) fifth abdominal segment, 1, spiracle, 2, verruciform sensilla; (H) caudal segment, 1, minute acanthae, 2, rima, 3, interspiracular process.

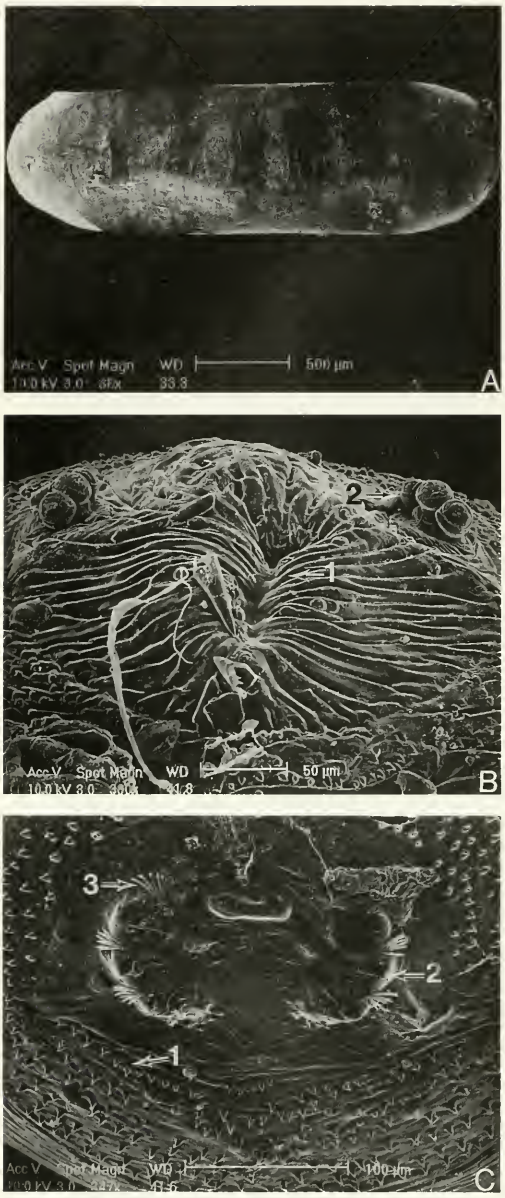

Fig. 4. Puparium of *Trupanea arizonensis*: (A) habitus, anterior end to right; (B) anterior end, 1, invagination scar, 2, anterior thoracic spiracle; (C) caudal segment, 1, minute acanthae, 2, rima, 3, interspiracular process.

(range, 15–24) florets, of which an average of only 1.6 ± 0.2 (range, 1–3) florets, or 9% (range, 4–17%), were damaged. No receptacles within these 14 infested flower heads was pitted by first-instar feeding.

Second instars fed solitarily at the distal ends of individual ovules or soft achenes within different florets of separate preblossom and open flower heads, respectively. Their mouthparts were directed towards the receptacles. Receptacles of 16 flower heads containing second instars were not pitted and averaged 3.4 ± 0.2 (range, 2.3–4.8) mm in diameter. These flower heads contained an average of 1.6 ± 0.2 (range, 1–3) second instars that had damaged an average of 1.8 ± 0.2 (range, 1–4) ovules, or 11% (range, 6–22%) of an average total of 17 ± 0.8 (range, 12–20) ovules per flower head.

Most third instars also confined their feeding to the same single, separate ovule or soft achene at the centers, and less commonly at the margins, of preblossom or open flower heads (Fig. 5D). Third instars fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles, and on the distal parts of the ovules or soft achenes, well above the receptacles (Fig. 5D). In 28 flower heads averaging 4.0 ± 0.1 (range, 3.1–5.0) mm in diameter and containing an average of 1.5 ± 0.2 (range, 1–5) third instars, an average of 1.6 ± 0.2 (range, 1–5) ovules were damaged, or 9% (range, 4–25%). Thus, each larva confined its feeding to the distal parts of a single floret, at most including corolla tube and contents, pappus, and upper part of the ovule (Fig. 5D); the ovule continued to grow and functioned as a nutrient sink (Harris and Shorthouse 1996) augmented by the larva which fed mainly on sap drawn to the cuplike depression in the distal end of the ovule (Fig. 5D). This mode of feeding is the least damaging to host-plant reproduction, as well as the most exquisitely evolved manner of sap-feeding yet reported among florivorous Tephritidae (Headrick and Goeden 1998). This manner of larval feeding, first reported by Headrick and Goeden (1990b), apparently is facultative, undetected, or absent in some florivorous species, e.g., *Paracantha gentilis* Hering (Headrick and Goeden 1990a, b), *Trupanea nigricornis* and *T. bisetosa* (Knio et al.

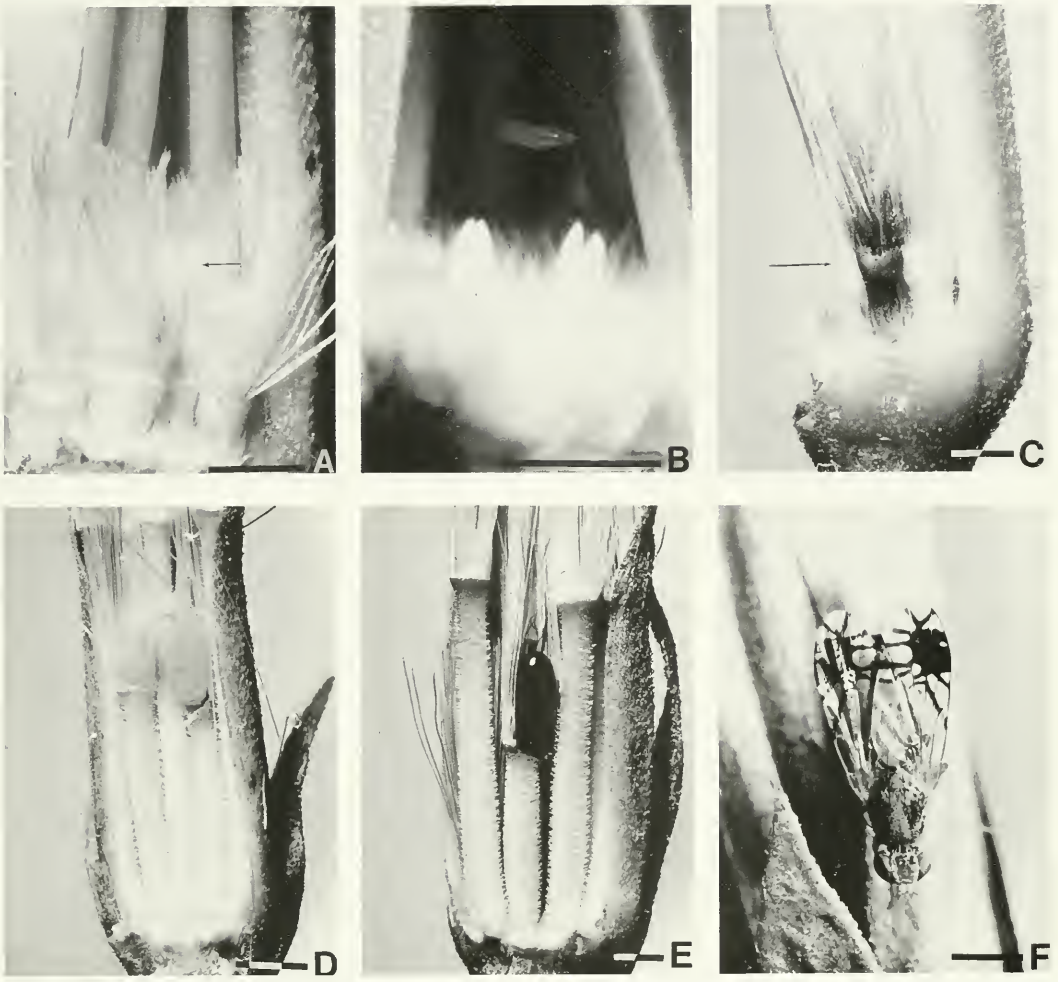

Fig. 5. Life stages of *Trupanea arizonensis* in or on *Trixis californica:* (A) one pair of eggs (arrow) inserted among immature florets in closed, preblossom flower head; (B) two pairs of eggs inserted among florets in closed, preblossom flower head; (C) first instar tunneling in single floret (arrow); (D) two third instars feeding on separate soft achenes; (E) single puparium atop stunted achene in flower head; (F) adult female at rest on flower head. Lines = 1 mm.

(1996b); although it also has been reported in some gallicolous species, e.g., *Aciurina thoracica* Curran (Headrick and Goeden 1993), and is facilitated by specialized mouthparts in larval Tephritinae (Headrick and Goeden 1990a, 1993, 1998).

Upon completing feeding, the larvae oriented their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 5E).

Pupa.—Flower heads containing puparia (Fig. 5E) contained the greatest amounts of damage produced by the seed-feeding larvae of *T. arizonensis*. The receptacles of 41 open and postblossom flower heads containing puparia averaged 4.4 ± 0.1 (range, 2.9–6.2) mm in diameter and bone an average total of 19.2 ± 0.6 (12–26) soft achenes, of which an average of 2.2 ± 0.3 (range, 1–9) soft achenes or 13% (range, 4–58%) were damaged. Again, no receptacles were fed upon. These heads contained an average of 1.8 ± 0.2 (range, 1–7) puparia. Most puparia of *T. arizonensis* were found near the centers of the flower heads, and all had their anterior ends facing away from

the receptacles, and their long axes were perpendicular to the receptacles (Fig. 5E).

Adult.—Adults (Fig. 5F) emerged from mature, postblossom flower heads, and were long-lived under insectary conditions, as 15 unmated males lived an average of 89 ± 14 (range, 11–194) days, and six virgin females averaged 126 ± 7 (range, 110–150) days. Like several other, monophagous and nearly monophagous congeners studied (Goeden 1988, Goeden and Teerink 1997, 1998), the longevities of these flies were among the longer averages and maxima for adults that we have recorded for native species of nonfrugivorous Tephritidae from southern California. Such longevities are commensurate with the aggregative type of life cycle ascribed below to this tephritid. The premating and mating behaviors of *T. arizonensis* were not studied in the field, and again, like most congeners that we have studied, adults would not mate in petri dish arenas otherwise so useful with many other, noncongeneric, nonfrugivorous species (Headrick and Goeden 1994).

Seasonal history.—The life cycle of *T. arizonensis* in southern California appears to follow an aggregative pattern in which the long-lived adults in reproductive diapause over-summer in riparian habitats and mountain meadows. They return to lower elevations in the fall, and following the onset of winter rainfall, aggregate on *Trixis californica* in the low-elevation Colorado Desert in winter (January–February) to mate and later to oviposit (March–April) (Headrick and Goeden 1994). A single annual generation is produced each year and most of the life span of *T. arizonensis* is spent as an adult.

Natural enemies.—*Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from individual puparia of *T. arizonensis* as a solitary, larval-pupal endoparasitoid; however, at least some of the other species of parasitoids reported from *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991) and *Trupanea conjuncta* (Goeden 1987), which co-occur in symphagy in the heads of *Trixis californica* (Goeden and Ricker 1989, Goeden 1997), probably also parasitize *T. arizonensis*.

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TWO NEW SPECIES OF *AGARODES* BANKS (TRICHOPTERA: SERICOSTOMATIDAE) FROM SOUTHEASTERN UNITED STATES

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Abstract.—Two **new species, *Agarodes logani,*** from the eastern panhandle of Florida, and ***Agarodes tuskaloosa,*** from west-central Alabama, are described, illustrated, and compared to congeners. The genus now totals twelve species, all restricted to eastern North America.

Key Words: Trichoptera, Sericostomatidae, *Agarodes,* new species, southeast

The genus *Agarodes* Banks is restricted to eastern North America and ranges from southern Canada to the southern United States (Ross and Scott 1974). *Agarodes* larvae prefer smaller, spring-fed streams with a medium current and sandy substrate but they have been occasionally collected in larger streams fed by surface water and in the sandy, depositional areas of lakes.

Ten species of *Agarodes* were previously recognized (Harris 1987) with all but *A. distincta* Ulmer and *A. grisea* Banks restricted to southeastern United States (Ross and Scott 1974). In Alabama, five species occur, *A. crassicornis* Walker, *A. libalis* Ross and Scott, *A. alabamensis* Harris on the Coastal Plain; *A. grisea* Banks in northern Alabama; and *A. stannardi* Ross in a restricted, northwestern region of the state. To this list from Alabama an apparently rare, new species is added, *A. tuskaloosa.* This new species is currently known only from the type locality, on a small, spring-fed stream at the northern edge of the Coastal Plain. In Florida, three species occur, *A. crassicornis* Walker and *A. libalis* Ross and Scott at scattered localities; and *A. ziczac* Ross and Scott known only from the type locality in the central panhandle region. To this Florida list, *A. logani,* a new species, is added. This species is currently known only from the type locality, a small spring-run in a deep ravine, in the eastern panhandle region. *Agarodes tuskaloosa* and *Agarodes logani* are members of the subgenus *Agarodes* Banks (Ross and Wallace 1974) based on the small antennal scape and slender mesal lobe of the maxillary palp. Both were collected with a black light.

Type material is deposited at the National Museum of Natural History, Smithsonian Institution, Washington D.C. Terminology follows that of Schmid (1980) and Ross and Scott (1974).

Agarodes logani Keth and Harris, new species

(Figs. 1, 4)

Diagnosis.—This species resembles *A. stannardi* but differs, primarily, in the elongate, strongly curved dorsomesal process of the mesal processes of the inferior appendage. The dorsomesal process (Fig. 1) of *A. logani* is about twice the length seen in *A. stannardi* (Fig. 2) and much more serrate ventrally. The female is very similar to *A.*

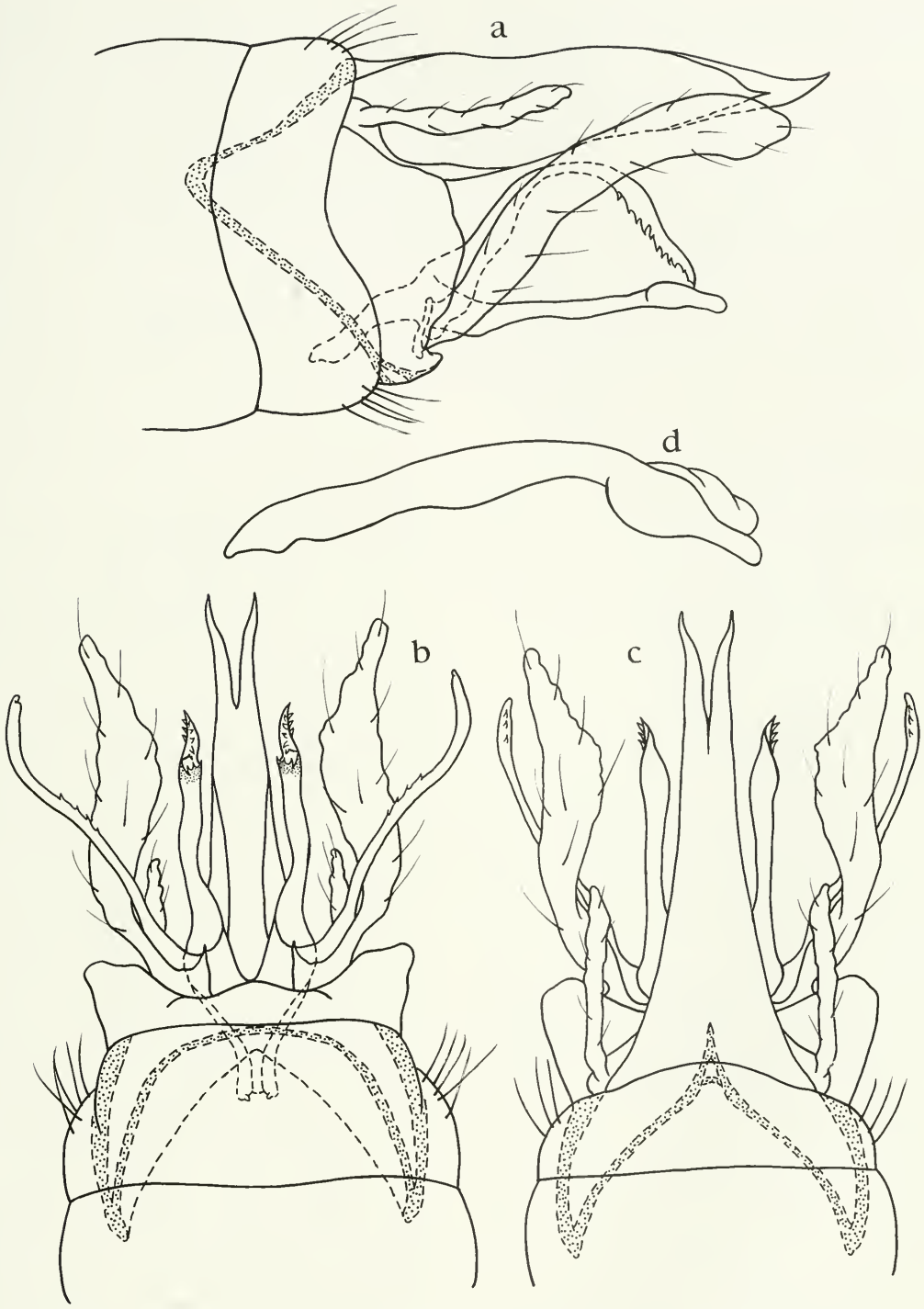

Fig. 1. ***Agarodes logani,*** male genitalia. a) lateral, b) ventral, c) dorsal, d) phallus.

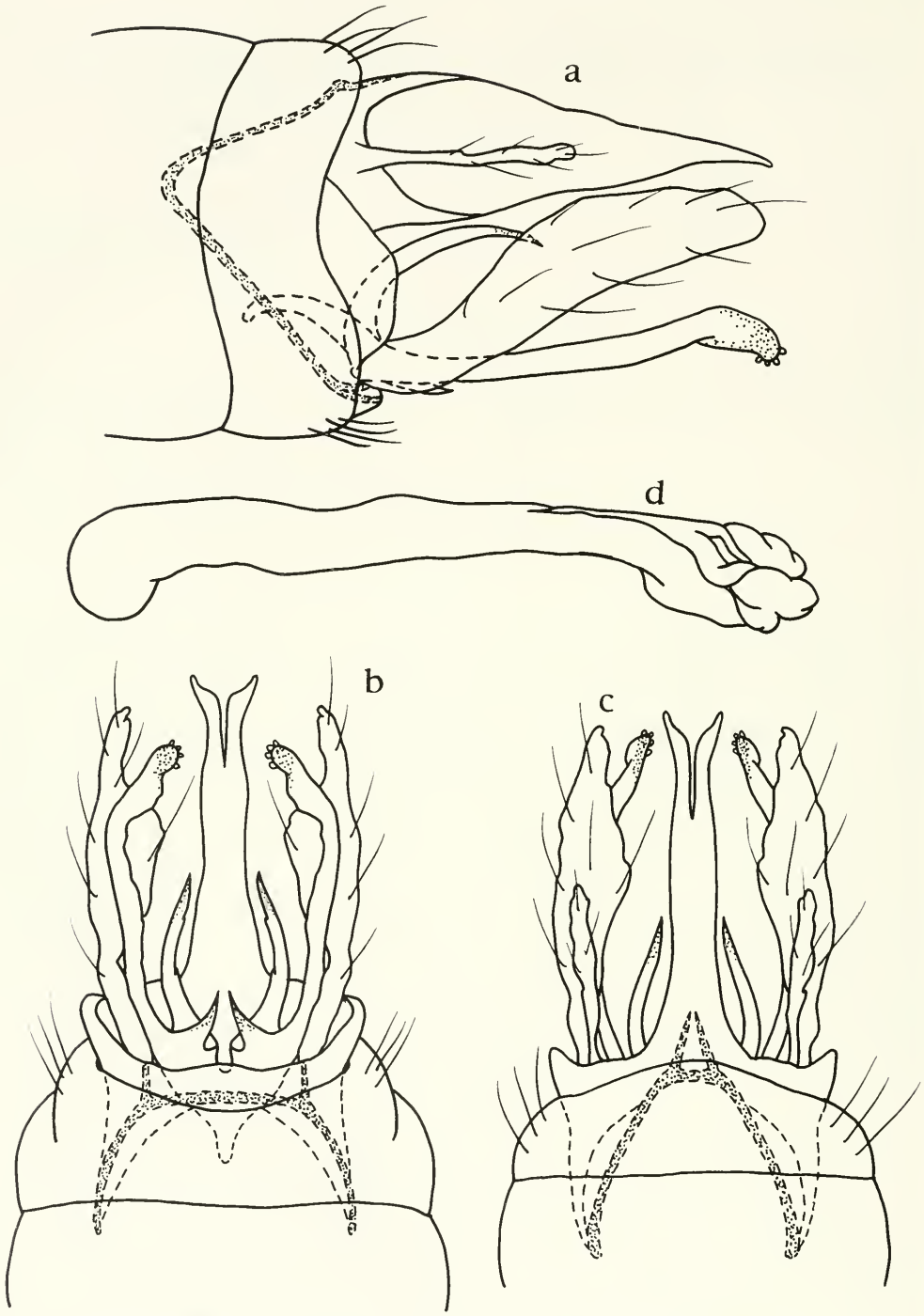

Fig. 2. *Agarodes stannardi,* male genitalia. a) lateral, b) ventral, c) dorsal, d) phallus.

stannardi differing only in the pair of short processes extending from apex of the dorsum of segment IX. These processes in *A. stannardi* are divergent and basally lobate in dorsal view (Fig. 3) and in *A. logani* narrow and lacking basal lobes (Fig. 4).

Male.—Length 9–11 mm. Body, legs, and head golden to dark brown. Antenna brown with 43 segments, scape small and rectangular. Labial palpus 0.9 mm long; maxillary palpus 0.5 mm in length, oblong, and bearing 2 small inner processes. Wings golden to dark brown; forewing with extensive peg-like setae in anal region and along M and Cu veins. Abdominal segment VIII annular. Segment IX inserted within segments VII and VIII, reduced, and dorsally fused with base of segment X. Segment X elongate and narrow in dorsal view, divided apically; in lateral view sinuate dorsally and lightly sclerotized, tapering to a point and curving slightly dorsad at apex. Genitalia as in Fig. 1 with preanal appendage narrow and elongate extending nearly half length of tergum X, curving dorsad. Inferior appendage uniform over entire length in lateral view; in ventral view united basally, slender anteriorly, widening midway, and narrowing posteriorly. Mesal processes bipartite; dorsomesal process over ¾ length of inferior appendage, slender and narrowing to acute apex with large, serrate, ventrad projections from ⅔ of length to apex and curving markedly ventrad in lateral view. Ventromesal process thin and nearly equal in length to dorsomesal process, divergent, curving markedly mesad at tip, slightly serrate distally at midlength and dorsally at apex. Phallus long and cylindrical, widening at membranous apex.

Female.—Length, color, and general structure as in male. Genitalia as in Fig. 4 with cerci long and contiguous, mesally merging with a short lobe. Apex of tergum IX having a pair of short processes projecting posteriorly from dorsum; processes narrow and fused basally, lacking basolateral lobes. Genital chamber narrow with margins folded, sclerotized, and curving mesad in ventral view, a pair of sclerous, scoop-like lobes diverging from base in dorsal view.

Immatures.—Unknown

Etymology.—Latin: of Logan, primary author's son

Holotype.—♂, Florida, Gadsden County, headwaters of Quincy Creek, 7 km. north Quincy at Florida A&M Research and Extension Center, N30°39′27″, W84°36′50″, 19 April 1994, Pescador and Rasmussen.

Paratypes.—Florida, same as above, 1 ♂; same, but N30°39′19″, W84°36′51″, 6 October 1993, Jones, Pecador, and Rasmussen, 1 ♀.

Distribution.—*Agarodes logani* is known only from the type locality. More specimens have been found in the same area including *Agarodes* larvae which, upon rearing, may be found to be *A. logani.*

Agarodes tuskaloosa Keth and Harris, new species

(Fig. 5)

Diagnosis.—This species resembles *A. stannardi* and the preceding new species, but it differs from *A. stannardi* in the much thinner inner process of the mesal process of the inferior appendage and from *A. logani* in the presence of a short basomesal process (Fig. 5). The dorsal and ventromesal processes of *A. tuskaloosa* are like those of *A. stannardi* but twice the length.

Male.—Length 11–13 mm. Body, legs and head golden to reddish brown. Antenna dark brown with 43 segments, scape small and trapezoidal. Labial palpus 1.0 mm long; maxillary palpus 0.6 mm in length, oblong. Wings light brown. Abdominal segment VIII annular. Segment IX inserted within segments VII and VIII, reduced, and dorsally fused with base of segment X. Segment X elongate and narrow in dorsal view, split apically; narrowing to elongate, acute apex in lateral view. Genitalia as in Fig. 5 with preanal appendage narrow, elongate, ⅓ length of tergum X, uniform over entire length in lateral view. Inferior appendage narrow basally, broadening toward apex in

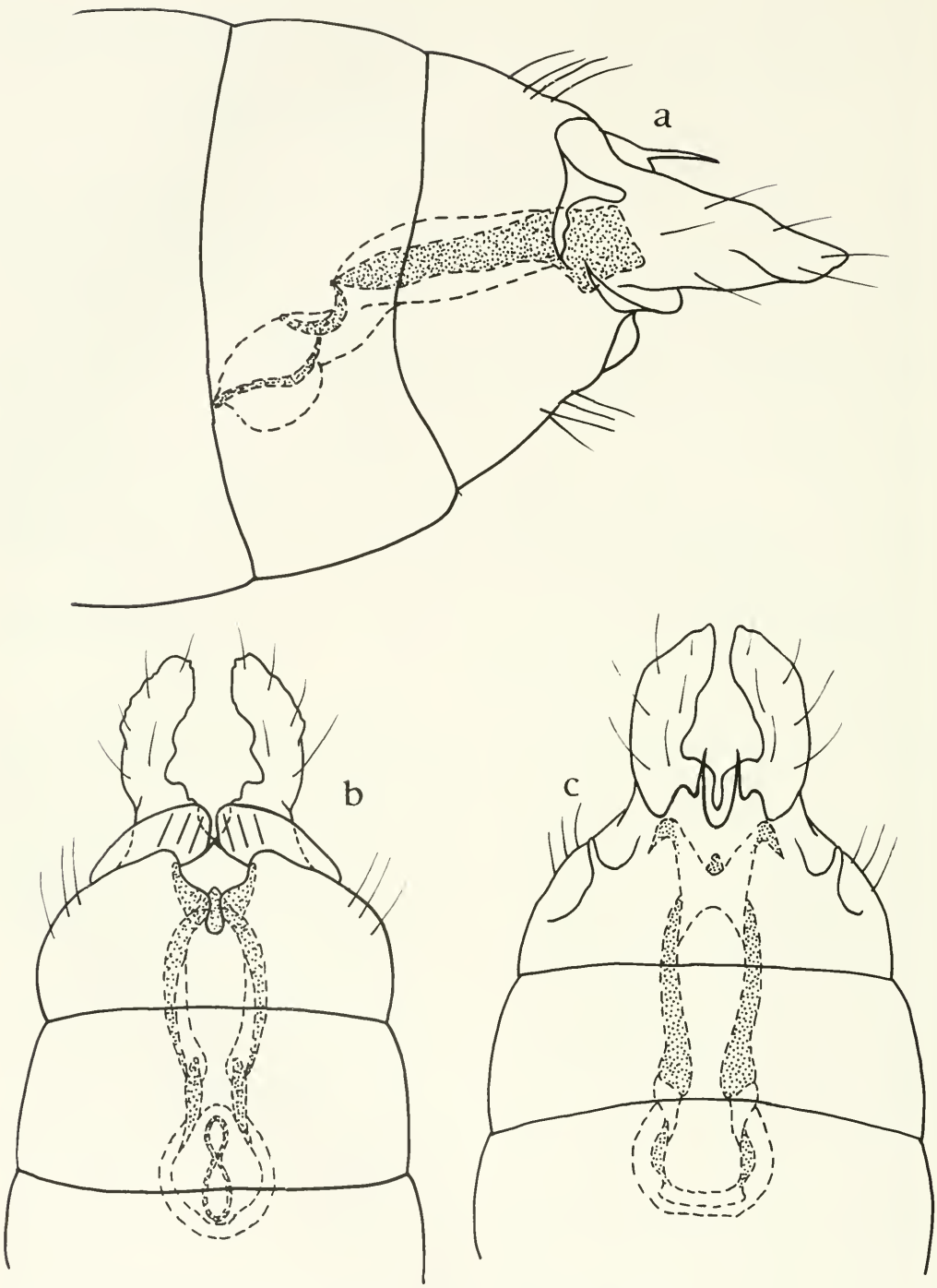

Fig. 3. *Agarodes stannardi*, female genitalia. a) lateral, b) ventral, c) dorsal.

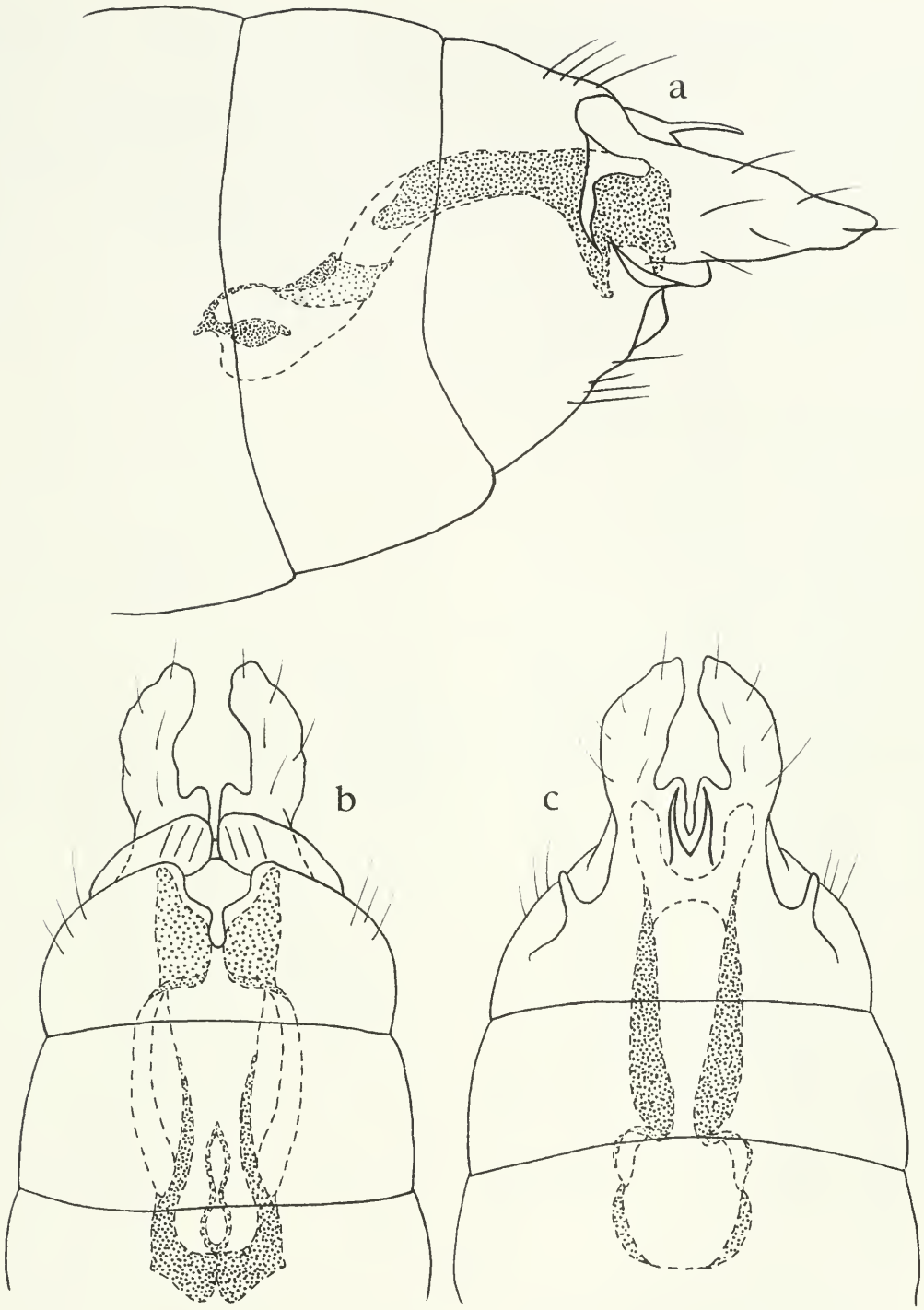

Fig. 4. *Agarodes logani*, female genitalia. a) lateral, b) ventral, c) dorsal.

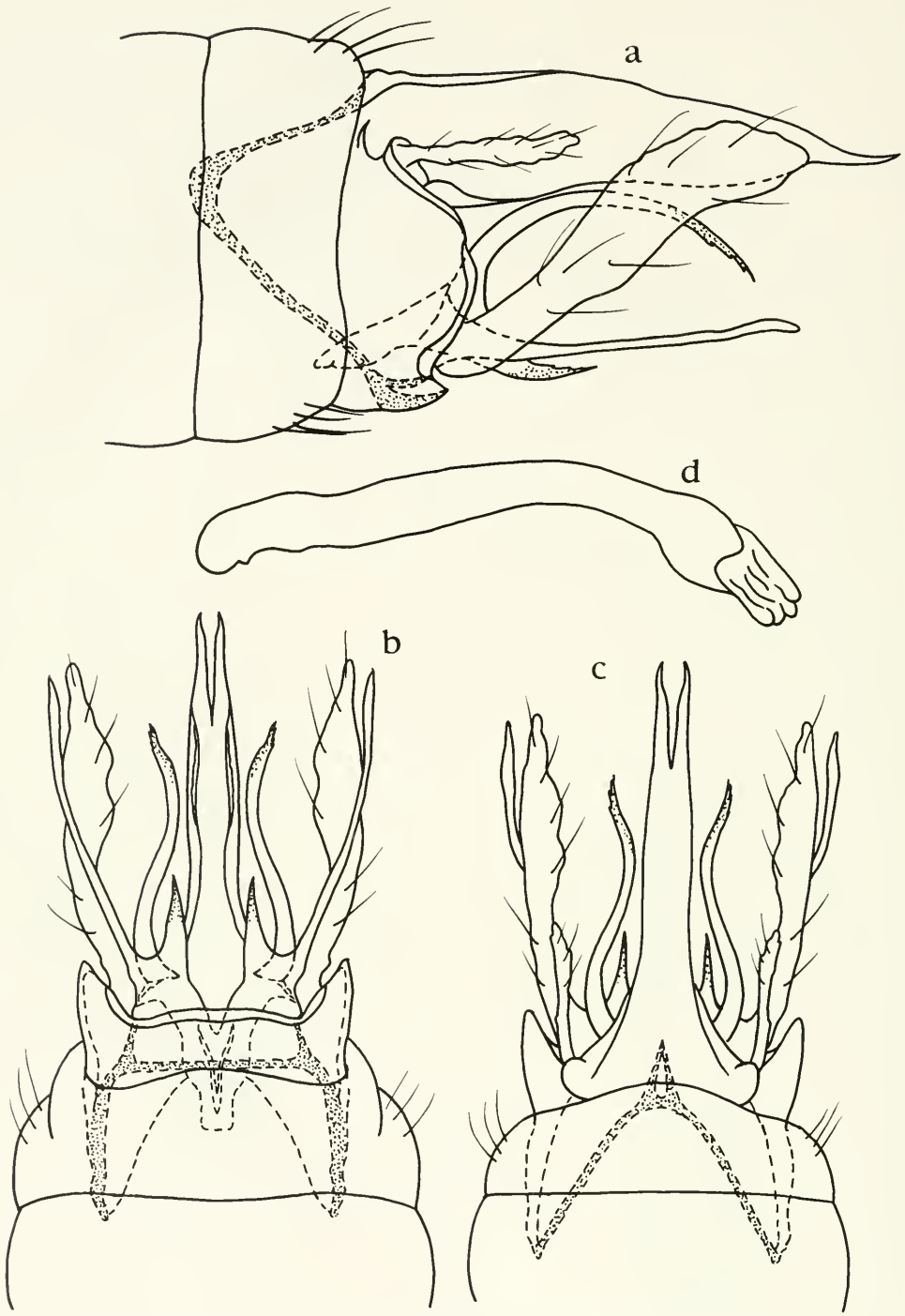

Fig. 5. ***Agarodes tuskaloosa***, male genitalia. a) lateral, b) ventral, c) dorsal, d) phallus.

lateral view; in ventral view slender and united basally, broadening ⅔ of length, and tapering to acute apex. Mesal processes tripartite; basomesal process short and acute with slightly serrate apex dorsally, dorsomesal process ¾ length of inferior appendage and strongly curved in lateral view, apex slightly serrate ventrally; inner process thin, uniform, and elongate. Phallus long and cylindrical, widening slightly at membranous apex.

Female.—Unknown

Immatures.—Unknown

Etymology.—Native American spelling: of Tuscaloosa region

Holotype.—♂, Alabama, Tuscaloosa County, Big Sandy Creek, 7.2 km. south of Coaling, on unmarked county road, 15 May 1991, Harris.

Paratype.—Alabama, locality and date as holotype, 1 ♂.

Distribution.—*Agarodes tuskaloosa* is known only from the type locality. Extensive collecting at the type locality and elsewhere in Big Sandy Creek has yielded no additional specimens.

Acknowledgments

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THE HIGHER CLASSIFICATION OF THE ALYDIDAE (HEMIPTERA: HETEROPTERA)

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Abstract.—Characters are taken from the literature and their derived states determined. The following higher classification of the Alydidae best agrees with the data: family Alydidae; subfamilies Alydinae and Micrelytrinae, the Alydinae with tribes Alydini and Daclerini; the Micrelytrinae with tribes Micrelytrini and Leptocorisini; the latter with subtribes Leptocorisidi and Noliphidi.

Key Words: Alydidae, higher classification, Leptocorisini, Micrelytrinae, Noliphini, Daclerini

Until 1965 the family Alydidae had been variously treated as a subfamily of Coreidae, or as a family in its own right. However, when treated as a family the habit of subfamilial treatment persisted, and the lower categories were considered tribes, not subfamilies (see Schaefer [1965] for the taxonomic history). In 1965 I presented evidence for family rank of the group, and recognized two subfamilies, Alydinae and Micrelytrinae, the latter with two tribes, Micrelytrini and Leptocorisini.

In the same year, Ahmad (1965) published his revision of *Leptocorisa* and its relatives. He treated this group as a subfamily, of status equal to Alydinae (*sensu mihi*) and Micrelytrinae (Micrelytrini *mei*). He discussed these three subfamilies very briefly, but did not give arguments for treating them as of equal rank. Ahmad and I had not seen each other's papers, and therefore neither of us could consider the higher-rank treatment of the other.

Since 1965, Ahmad's view has prevailed, with a lapse in 1979, when Ahmad et al. (1979) treated Leptocorisini and Micrelytrini as tribes in the subfamily Leptocorisinae. Nevertheless, most post-1965 authors treated the three groups as subfamilies, perhaps because Ahmad's (1965) study of the Leptocorisinae (*sensu suo*) was more detailed than mine of the entire Alydidae. Indeed, I myself subsequently treated the three groups as subfamilies (see, for example, Schaefer 1972, 1980, Schaefer et al. 1989, but see Schaefer 1996); most notably, the three subfamilies are recognized in the catalog of Nearctic Heteroptera (Froeschner 1988). (Note: the change by Henry and Froeschner [1992] from Leptocorisinae to Leptocorinae is surely incorrect: the generic name is *Leptocorisa,* not *Leptocoris* [which is a genus in Rhopalidae].)

In 1993, Li and Zheng published a study of alydid phylogeny. In it they concluded "that Schaefer's (1965) division of this family into two subfamilies—Alydinae and Micrelytrinae—is reasonable." Their "cladograms do not support Ahmad's (1965) and some other authors' contention that the Alydidae be divided into three subfamilies—Alydinae, Leptocorisinae, and Micrelytrinae" (quoted from the English abstract of Li and Zheng [1993]). Since the

appearance of this paper, Prof. Zheng has most generously provided me with an English translation of it.

Li and Zheng (1993) discuss and illustrate many characters in some detail, thus adding substantially to the already rich literature on Alydidae (see references in Table 1). Accordingly, I have extracted characters from this literature and have attempted to determine their derived states, in an attempt to establish better the Alydidae's higher classification.

Methods

I extracted from the literature on the Alydidae characters whose states could be tabulated and whose polarities for the most part could be determined. All these characters are ones important in the higher systematics of Coreoidea and, indeed, of Pentatomomorpha (the heteropteran infraorder to which Coreoidea belongs; see Henry 1997). Sample size is of course a problem; all genera and many species of Alydinae are described in Schaffner's dissertation (1964), but only for the Leptocorisini are all members of the group treated and their morphology described, in Ahmad's (1965) monograph. In particular, the Micrelytrini need revision, with attention given to morphological features of systematic importance in other alydids.

In polarizing the character states I take the Coreidae as the outgroup. Henry (1997) presents convincing evidence that this family is the sibling group of Alydidae. Other arguments for my polarizing occur in the references and in footnotes to Table 1.

Results and Discussion

Twenty-eight characters and their states are in Table 1 (where I anticipate my conclusions by treating Micrelytrini and Leptocorisini as tribes and Alydinae as a subfamily). Of these characters, I polarized 23; three of the remainder I could not polarize (Distribution, Host plants, Rostral segments); one (Scent gland auricle) is ambiguous; and it is not clear to me if bifid (Micrelytrini) and trifid (Leptocorisini) medial projections of the genital capsule are separate advances over the (primitive) alydine condition, or whether the trifid condition is a further advance over the bifid (in which case, this character would group Micrelytrini and Leptocorisini together).

Thirteen of the characters are autapomorphies of one of the three groups. These autapomorphies are not the only ones defining these groups, of course, because I was not seeking autapomorphies in the literature. Nevertheless, the fact that Alydinae has eight autapomorphies, and the other two groups have fewer (Micrelytrini: 4; Leptocorisini: 1), supports the subfamily status of Alydinae.

Within the Alydinae, Ahmad et al. (1979) created a tribe, Daclerini, for the published genus *Daclera* and for another, unpublished genus. Although they present the new tribe as "MS," it is briefly described in their key and therefore appears to be valid. I have not seen specimens either of *Daclera* or of the undescribed genus. However, Li and Zheng (1993) write that *Daclera* has many apomorphies not shared with other Alydinae. Therefore I treat Daclerini as a tribe in Alydinae, pending further study.

Within the subfamily Micrelytrinae, Micrelytrini and Leptocorisini share six apomorphies (seven, if the median projection condition is synapomorphic; see above), more than either group shares with Alydinae (Micrelytrini and Alydinae: 2; Leptocorisini and Alydinae: 2). Three of these four synapomorphies shared by Alydinae and either Micrelytrini or Leptocorisini are head characters. The states of these characters vary considerably in the Coreoidea (Schaefer 1965), and their common possession in Alydinae and one of the other tribes may therefore be homoplasious. If one accepts that eight autapomorphies is a reasonable argument for subfamily status for Alydinae, then six synapomorphies should support subfamily status for Micrelytrini plus Leptocorisini. Moreover, four of these six synapomorphies are characters of the

Table 1. Differences and similarities among Micrelytrini, Leptocorisini, and Alydinae. Apomorphic states in **boldface**.

	Micrelytrini	Leptocorisini	Alydinae	Reference
Distribution	tropical, subtropical	tropical, subtropical	tropical, subtropical; some temperate	Schaffner 1964, Ahmad 1965
Host plants	Graminae (?)	Graminae	Leguminosae	Schaefer 1979
Head				
Midcephalic sulcus	**deep**	**deep**	shallow or absent	Li and Zheng 1993
Head constricted basally	**yes**	rarely	**yes**	Li and Zheng 1993
Head with "collar"	no	**yes**	**yes**	Schaefer 1965
Ocelli on tubercle	**yes**	rarely	**yes**	Li and Zheng 1993
Paraclypei well developed	sometimes	**yes**	no	Li and Zheng 1993, Ahmad 1965
Rostral segments	2 > 3 + 4; 4 = twice 3	2 < 3 + 4; 4 = 3	2 < 3 + 4; 4 > 3, rarely twice 3	Ahmad 1965, Schaefer, unpubl.
Thorax				
Hind femur	not armed	not armed	**spined or with stiff setae**[a]	Schaffner 1964, Ahmad 1965
Hind tibia	straight, untoothed	straight, untoothed	**usually curved and with ventral tooth**[a]	Schaffner 1964, Li and Zheng 1993
Forewing media	**coriaceous basally in membrane**	**coriaceous basally in membrane**	not coriaceous	Li and Zheng 1993
Forewing costa	not fused to radius and media	not fused to radius and media	fused[b]	Schaefer 1965, Li and Zheng 1993
Scent gland peritreme: lateral and anterior auricles fused	variable (no: Schaefer 1965; yes: Li and Zheng 1993)	no	yes	Schaefer 1965, Li and Zheng 1993
Abdomen				
Trichobothria (5th sternum)	in a triangle	in a triangle	**in a line**[c]	Schaefer 1965, 1975
Male genital capsule[d]				
Ventral rim	**with spine**	without spine[e]	without spine	Schaefer 1980
External opening	posterior	**dorsal**	**dorsal or postero-dorsal**	Schaefer 1980
Dorsal wall	sclerotized	sclerotized	**membranous**	Schaefer 1980, Schaefer et al. 1989
Median projection	**bifid**	**trifid**	single	Schaefer 1980, Schaefer et al. 1989
Cuplike sclerite with lateral projections	no	no	yes	Schaefer et al. 1989
Segment 10	**sclerotized dorsally**	**sclerotized dorsally**	membranous dorsally	Schaefer 1980
Paramere	apex not tuberculate	apex not tuberculate	**apex tuberculate**	Ahmad 1965, Li and Zheng 1993

Table 1. Continued.

	Micrelytrini	Leptocorisini	Alydinae	Reference
Male aedeagus				
Vesica	**not slender, coiled**[f]	**not slender, coiled**[f]	**slender, straight**[f]	Schaefer 1965, Ahmad 1965, Li and Zheng 1993
Conjunctiva	**laterally with pair of asymmetrical appendages**	**laterally with pair of asymmetrical appendages**	without these appendages	Schaefer 1965, Ahmad 1965, Li and Zheng 1993
Phallosoma	**dorsally with pair of apically directed appendages**	**dorsally with pair of apically directed appendages**	without these appendages	Schaefer 1965, Ahmad 1965, Li and Zheng 1993
Female genitalia				
9th paratergite	**divided**	not divided	not divided	Schaefer 1965
2nd valvula	**partly membranous**	sclerotized	sclerotized	Schaefer 1965
Ring sclerites	1 pair	**2 pairs**	1 pair	Schaefer 1965
Ring-sclerite sacs	**1 median sac**	1 pair[g]	1 pair	Schaefer 1965

[a] Curved and armed femora and tibia are uncommon in Coreoidea (except some Meropachydinae and some male Coreinae).

[b] Fusion of wing veins appears *ipso facto* to be more advanced than nonfusion.

[c] The posterior abdominal trichobothria in Coreoidea are usually in a triangle (except Rhopalidae) (Schaefer 1975).

[d] These features vary independently of one another (Schaefer 1980), and therefore may be treated as separate characters.

[e] Spine is present in at least one leptocorisine (discussion in Schaefer 1980, p. 126).

[f] According to Li and Zheng (1993), the apomorphic state of Alydinae differs from the apomorphic state of Micrelytrinae.

[g] Ahmad (1965) writes that Leptocorisini have 0–4 pairs of "intervalvular sclerites"; I believe these are not the same as the sacs associated with the ring sclerites.

male genitalia, a character complex always useful in heteropteran higher classification; common possession here is unlikely to be homoplasious In addition, other characters support the uniting of these two groups as a subfamily; these characters and the arguments based upon them, are not easily tabulated: see Schaefer (1965).

Li and Zheng (1993) comment upon the antlike fascies of Alydinae, treating it as an autapomorphy of the group. It is true that immature alydines are antlike, but so are the adults of several Micrelytrini. In fact, there are two groups of Micrelytrini, one of somewhat or quite elongate insects, and the other of smaller often antlike insects (Schaefer 1996). Members of both groups occur in both the New and Old World tropics. By chance, Li and Zheng (1993) took as their representatives of Micrelytrini *Marcius* and *Paramarcius,* both members of the somewhat elongate (and nonantlike) group.

Of great interest would be a study of the phylogenetic relationships among these four groups (New World and Old World antlike and elongate micrelytrines), between the antlike micrelytrines and the Alydinae (whose nymphs are antlike), and between the elongate micrelytrines and the Leptocorisini (most of whose genera are Old World tropical; the Noliphidi are somewhat elongate and the Leptocorisidi are very elongate). I discussed some of these relationships earlier (Schaefer 1972).

Classification

As a result of this work, I suggest the following classification, in which the tribes of Ahmad's (1965) Leptocorisinae are reduced to subtribes.

Family Alydidae Amyot et Serville 1843
Subfamily Alydinae Amyot et Serville 1843
Tribe Alydini
Tribe Daclerini
Subfamily Micrelytrinae Stål 1867
Tribe Micrelytrini Stål 1867
Tribe Leptocorisini Stål 1870
Subtribe Leptocorisidi Stål 1870
Subtribe Noliphidi Ahmad 1965

Note: Based on their cladistic analysis, Li and Zheng (1993) suggest that *Acestra,* a genus placed uneasily in the Micrelytrini (see discussion in Li and Zheng [1993]), be removed from Micrelytrini and raised to tribal rank in the Micrelytrinae; they do not do this formally. Also, as I mentioned above, Li and Zheng (1993) found autapomorphies in *Daclera,* the only described genus now in Daclerini. These two genera should be studied more closely, as should the Micrelytrini as a whole.

Acknowledgments

I am deeply grateful to Zheng Le-yi for translating the Li and Zheng (1993) paper for me. Without his kindness and generosity, my paper had been difficult to undertake and impossible to complete satisfactorily. I thank also Ann Harlan for word-processing this paper and for being a favorite daughter.

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OBSERVATIONS ON TWELVE FAMILIES OF HOMOPTERA IN MACAU, SOUTHEASTERN CHINA, FROM 1989 TO THE PRESENT

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Abstract.—The insect species found in present day Macao are largely those feeding upon small numbers of remnant agricultural plantings or on those plants representing the subtropical evergreen broad leaf forest or remnants of the tropical monsoon rainforest as agricultural crops are only grown on a small scale. Records of 37 species of Homoptera of the Aleyrodidae, Aphididae, Cicadellidae, Cicadidae, Coccidae, Delphacidae, Diaspididae, Flatidae, Fulgoridae, Margarodidae, Pseudococcidae and Psyllidae are listed for the Portuguese territory of Macao of which 27 are new records.

Key Words: Macao, Homoptera, faunal list

In the early part of the present century a number of homopteran species were listed as occuring in Macao and Hong Kong as well as part of the Guangdong Province of mainland China all of which was known at that time as South China (Kirkaldy 1909). Rice was considered the main agricultural crop and farming was the chief livelihood of most of the people in south east China. The land area that John C.W. Kershaw (Kirkaldy 1909) collected insects on was considered an island at that time but it is now connected to the mainland of China and today is considered the peninsula. The majority of the collections made in this study, however were taken from the islands of Taipa and Coloane which are connected to the peninsula either by two bridges (Taipa) or a causeway (Coloane) which did not exist in the early part of the century. Many of the insect species noted to occur in Macao at the beginning of the century may now be non-existant. We were unable to find evidence, for example, of the planthoppers described by Frederick Muir (1913) because of modernization and construction of hotels and apartment complexes that have replaced agricultural farmlands. Easton and Pun (1997) discussed the species of true bugs in the region and here we discuss the Homoptera.

MATERIALS AND METHODS

Insects were sampled routinely from the walls of window-lit buildings (Taipa island) that are often illuminated at night. Other insect groups less sensitive to light, such as the cicadas other than those in the genera *Cryptotympana*, and *Huechys*, as well as the Flatidae, Fulgoridae and the scale insects, were sampled with an insect net from trees, shrubs and grasses in forested areas on the islands of both Coloane and Taipa as well as from the peninsular area connected to the Guangdong region of China. The names of the plant hosts follow the Macau Catalogue of plants and their addenda (1991). Voucher specimens of the Homoptera named here are housed in the Entomology Museum of the Agrarian Services on Coloane (Seac Pai van Park) under the curatorship of the second author.

List of Species

HOMOPTERA

Aleyrodidae

Aleurocanthus spiniferus (Quaintance), orange spiny whitefly. No date, collector unknown, NEW RECORD, Coloane Island, Macao, ex. *Ficus rumphi*, *Rosa chinensis*. Mound and Halsey (1978) list it from India, Sri Lanka, Taiwan, Thailand, Malaysia, Philippines, Sumatra, Japan, and Hong Kong, while Peng and Liu (1992) report it from the Fujian, Guangxi, Henan, Hunan, Jiangsi, and Zhejiang provinces of China.

Trialeurodes vaporariorum (Westwood), greenhouse whitefly. No date, collector unknown, NEW RECORD. Coloane Island, Macao, ex. *Brassica oberacea*, *Citrus medica* and *Hybiscus rosa-sinensis*. Mound and Halsey (1978) list it from Malaya, India, Sri Lanka, Hawaii, New Guinea, New Zealand and most of the provinces of mainland China.

Aphididae

Aphis gossypii Glover, cotton or melon aphid. 5 Dec 1992, PWW leg. NEW RECORD, Coloane Island, ex. *Althaea rosea*, *Capsicum frutescens*, *Chrysanthemum morifolium*, *Citrullus lanatus*, *Colocassia esculenta*, *Cucurbita moschata*, *Dianthus caryophyllus*, *Hibiscus rosa-sinensis*, *Lilium japonicum*, *Litchi chinensis*, *Phaseolus radiatus*, *Psidium guajava*, *Punica granatum* and egg plant, *Solanum melongena*. It has been reported in Hong Kong (Lee and Winney 1981) and is widely distributed in China (Peng and Liu 1992).

Aphis nerii Boyer de Fonscolombe, nerium or oleander aphid. 5 Dec 1992, PWW leg, NEW RECORD, Coloane Island, Macau, ex. *Asclepius curassavica*, *Nerium indicum*. Raychaudhuri (1980) lists it throughout India and Japan, Java, Korea, and Taiwan. In Hong Kong, Lee and Winney (1981) report it common during winter months when it feeds on the shoots and leaves of oleander. Peng and Liu (1992) list it from Guangdong, Guangxi, Hunan, and Jiangsu provinces of China.

Formosaphis micheliae Takahashi. 21 March 1995, PWW leg. NEW RECORD, Coloane Island, Macao, ex. white jade orchid tree, *Michelia alba* and *M. champaca*. Blackman and Eastrop (1994) record it from Japan and Taiwan and Lee and Winney (1981) found it in Hong Kong.

Myzus persicae (Sulzer), green peach aphid. No date or collector, NEW RECORD, Coloane Island, Macao, ex. *Brassica chinensis*, *B. oberacea* and *Prunus persica*. This is considered a cosmopolitan temperate species and it is more common during winter months in Hong Kong with populations declining after April (Hill et al. 1982). It is widely distributed in China.

Neophyllaphis podocarpi Takahashi, buddhist pine aphid. 9 Feb 1995, PWW leg. NEW RECORD, Coloane Island, Macao, ex. *Podocarpus macrophyllus*. Distribution includes Malaysia, Taiwan, Hong Kong, Japan and the Guanxi, Hunan, Jilin, and Zhejiang provinces of China (Peng and Liu 1992).

Shivaphis celti B. Das. 17 March 1994, PWW leg. NEW RECORD, Coloane Island, Macao, ex. *Celtis sinensis*. Distribution includes Korea, Japan, India, Taiwan, Hong Kong and the Fujian, Guangdong, Guangxi, Guizhou, Hebei, Hunan, Jiangsu, Liaoning, Shandong, Sichuan, and Yunnan provinces of China (Peng and Liu 1992).

Tinocallis kahawaluokalani (Kirkaldy), crepe myrtle aphid. 27 Oct 1993, PWW leg. NEW RECORD, Coloane Island, Macao. ex. *Lagerstroemia indica*. This species is also found in India, Taiwan, Japan, and Hawaii (Raychaudhuri 1980).

Cicadellidae

Lodiana brevis (Walker), yellow-banded leafhopper. 9 Dec 1993. Ng Wai Man leg. NEW RECORD, Coloane Island, Macao, ex. *Cinnamomum camphora*, *Ficus microcarpa* and *Euphoria longan*. In Hong Kong Lee and Winney (1981) reported it from *Citrus* sp. Distribution includes the Guang-

dong, Guizhou, and Yunnan provinces of China as well as India, Taiwan, Malaysia, Thailand, and Japan (Datta 1988).

Nephotettix virescens (Distant), green rice leafhopper. No date or collector, NEW RECORD, Coloane Island, Macao, ex. *Citrus* sp., *Bambusa* sp., and *Saccharum officinarum*. There are records of it from rice in the Tai Lung farm insect collection in Hong Kong and Hill (1975) lists it as a pest of rice in India and China.

Petalocephala chlorocephala Walker. 4 Sept 1993, Ng Wai Man leg, NEW RECORD, Coloane Island, Macao, no host data.

Tettigoniella spectra (Distant), rice white leafhopper. 15 Sept 1992, Ng Wai Man leg, NEW RECORD, Coloane Island, Macao, ex. *Morus alba*, *Oryza sativa*, *Saccharum officinarium*. Distribution includes Taiwan, India, and Japan as well as the Guangdong and Hunan provinces of China (Peng and Liu 1992).

Another species of leafhopper, *Dryadomorpha pallida* Kirkaldy has not been collected in our study but Webb (1981) reported it from Macao and Hong Kong as well as the neighboring areas of India, Bangladesh, Taiwan, Japan, Laos, and the Philippines.

Cicadidae

Cryptotympana atrata (F.), large brown cicada. 20 June 1994. Cheong Chi Kong leg, Coloane island, Macao, ex. *Melia azedarach*, *Morus alba*, *Tectonis grandis*. Emergence of adults occurs from late May through early July in general but emergence on Taipa Island in 1998 was earlier (May 15). Distribution includes Hong Kong, the provinces of Guangdong, Hebei, and Zhejiang of China (Wu 1935) as well as Malaysia, Japan, and Taiwan.

Cryptotympana mandarina Distant. May 1997, 15 May 1998, ERE leg, Taipa Island, Macao. Kershaw (1903) is believed to be the first to record it from Macao while Kirkaldy (1909) reported it from Hong Kong. Nymphal skins have been observed on the trunks of various trees such as *Acacia confusa* and *Casuarina equisetifolia* in the municipal cemetary on Taipa island (Easton 1992) as well as the foxglove tree, *Paulownia fortunei* on Guia Hill of Macao peninsula in May, 1997 and on *Hibiscus tiliaceus* near the Monte Forte, Fortress, May 10, 1998. Emergence holes near the base of the trees indicated where the nymphs left the soil. Watery fluid has been observed emitting from the anal region of resting adults on Taipa Island suggesting that they had recently emerged from the ground. As feeding in adults has not been documented, the watery fluids may have accumulated while the nymphs were underground and release may be necessary before sound production can take place. Distribution also includes the Guangdong and Hainan provinces of China and Taiwan.

Chremistica ochracea (Walker). 23 May 1995, 10 May 1998, ERE leg, Taipa Island, Macao. Hayashi (1977) recorded this species from Macao, and Hill et al. (1982) illustrated it as the green clearwing cicada under the genus *Dundubia* in Hong Kong. Distribution also includes Taiwan and the Guangdong region of China.

Gaeana maculata Walker, yellow-spotted black cicada. 14 April 1994, Ng Wai Man leg, Coloane Island; 7 May 1998, ERE leg, Guia Hill, Macao peninsula. In the Seac Pai Van agricultural park on Coloane Island, nymphs were observed emerging as early as March 25 (Easton 1992). It has not been observed on Taipa island suggesting certain food plants may be necessary for nymphal development. In Hong Kong, Cheung and Marshall (1973) reported it from *Schinus terebinthiofolius*, Christmas berry tree, and *Paulownia tormetosa* and in Macao the senior author has observed it among the foliage of *Pawlownia fortunei* on the Guia Hill. Wu (1935) recorded it from Myanmar (Burma), Assam area of India, Vietnam, and Guangxi Province of China.

Huechys sanguineus (DeGeer), red-nosed cicada. 31 August 1992, Ng Wai Man leg, Coloane Island, Macao. Kirkaldy (1909)

first reported this species from Macao and Hong Kong. From 1989–1997 emergence from the ground has always been later in the year than with the former species and from September through December (Easton 1991). In 1998 however an emergence of 15–20 individuals was observed in an arboretum on Coloane island on May 10. Specific food plants have not been associated with nymphal feeding.

Mogannia hebes (Walker), grass cicada. 9 June 1994, ERE leg, NEW RECORD, Taipa Island on shrub on university campus; June 1996, May 1998, ERE leg, Seac Pai Van Agricultural Park, Coloane Island. Kirkaldy (1909) was probably the first to record it from Hong Kong, and Hayashi (1976) described its feeding on the stems of *Miscanthus* grass where females oviposit into stems and leaf midribs from April to June. Distribution includes Korea, India, Myanmar, and the Chejiang, Fujian, Guangdong, Guangxi, Jiangsi, Hunan, Sichuan, and Yunnan provinces of China.

Mogannia nasalis (White). 25 May 1966, ERE leg, Taipa Island, Macao on tree foliage along hiking trail in thickly forested hillside. This species was first recorded in Macao and Hong Kong by Kirkaldy (1909). It is also found in the Assam area of India.

Platypleura hilpa Walker, spotted brown cicada. 2 August 1992, PWW leg, Coloane Island, Macao. Nymphs were observed emerging at night near the trunks of *Casuarina equisetifolia* trees near the municipal cemetary on Taipa Island (Easton 1992). Kirkaldy (1909) reported it from Hong Kong and Macao, and it is also found in the Guangdong and Hunan provinces of China (Peng and Liu 1992).

Coccidae

Ceroplastes ceriferus (Fabricius), indian wax scale. 18 Dec 1992. PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Cinnamomum camphora*, *Melastoma sanguineum*, *Michelia figo*, *Morus alba*. Tang (1991) listed it from Australia and Hawaii and it is also found in Japan, India, Sri Lanka and provinces of China south of the Yangtze River.

Saissetia coffeae (Walker), helmet or hemispherical scale. 19 Jan 1988, PWW leg, NEW RECORD, Coloane Island, Macao, ex. Fukien tea, *Carmona microphylla* and sago palm, *Cycas revoluta*. Hill (1975) listed citrus, guava and mango as alternate hosts but mainly it is found on coffee plants and widespread in the tropics including southeastern Asia.

Delphacidae

Nilaparvata lugens (Stål), brown planthopper of rice. 22 Oct 1997, ERE leg, NEW RECORD, Taipa Island on window ledges and outside on floors of university campus buildings illuminated by lights. According to Hill (1975) and Wada et al. (1987), *N. lugens* invades Japan with the monsoon winds every year from China, so the large numbers (1,000+) observed in Macao over a brief period of 1–2 days suggests that the insects migrated from the neighboring Guangdong Province since rice is not grown commercially locally in Macao as a crop. In Malaysia and Indonesia, it is a major pest of rice and produces a browning effect on the plants known as "hopperburn." Lee and Winney (1981) also report it from *Gladiolus gandavensis* in Hong Kong. Yang (1989) gives its distribution as Australia, New Guinea, India, Korea, Taiwan, Philippines, Vietnam, and the Pacific islands of Fiji, Guam, Yap, and Palau, while Kuoh et al. (1983) list it from Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hebei, Henan, Honan, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Shandong, Shanxi, Yunnan, and Zhejiang Provinces in China.

Other species of Delphacidae reported earlier by Muir (1913), such as *Belocera sinensis* Muir, *Phyllodinus macaoensis* Muir, and *Tropidocephala saccharivorella* Matsumura, were not collected in this study and may no longer be found locally due to

the urbanization which has replaced agricultural crops.

Diaspididae

Aulacaspis rosarum Borchsinius, Asiatic rose scale. No date or collector, NEW RECORD, Coloane Island, Macao, ex. *Rosa chinensis*. Distribution includes the Fujian, Guangdong, Guangxi, Hunan, Jiangsu, Jiangxi, Shandong, Sichuan, Yunnan, and Zhejiang provinces of China (Peng and Liu 1992).

Aulacaspis yabunikkei Kuwana. 21 April 1988, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Cinnamomum camphora*. In Hong Kong, Lee and Winney (1981) also record it from pond spice, *Litsea glutinosa*. Distribution includes Japan and the Guangdong, Guizhou, Hunan, Sichuan, Yunnan, and Zhejiang Provinces of China (Peng and Liu 1992).

Hemiberlesia pityosophila Takagi. 7 June 1988, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Pinus mansoniana*.

Lepidosaphes laterochitinosa Green. 20 May 1997, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Osmanthus fragrans*, Kwai-Fah. In Hong Kong there are records of it from this host as well as *Schefflera octophylla*, Ivy tree, in the Tai Lung Farm insect collection.

Parlatoria pergandii Comstock, chaff scale. 23 Feb 1993, Yau H.C. leg, NEW RECORD, Coloane Island, Macao, ex. *Jasminium sambac* and *Citrus* sp. Distribution in the world is widespread, but in Asia it has been recorded from Australia, New Zealand, Japan, India, Philippines, Taiwan, and from the Anhui, Fujian, Guangdong, Guangxi, Hainan, Hebei, Henan, Hubei, Hunan, Jiangsi, Jiangsu, Liaoning, Qinghai, Shanxi, Shaanxi, Shanghai, Sichuan, Yunnan, and Zhejiang Provinces of China (Peng and Liu 1992).

Pseudaulacaspis cockerelli (Cooley), oyster or oleander scale. 7 May 1988, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Michelia alba*, *M. figo* and coconut palm, *Cocos nucifera*. In Hong Kong, there are also records from bamboo palm, *Chrysalidocarpus lutescens* (Lee and Winney 1981). Its distribution includes Thailand, Taiwan, and the Guangdong, Hubei, Hunan, Jiangsu, Jiangxi, Shandong, Sichuan, Yunnan, and Zhejiang provinces of China (Peng and Liu 1992).

Flatidae

Lawana imitata (Melichar), white moth bug. 18 July 1991, PWW leg, Coloane Island, Macao, ex. *Bauhinia* sp., *Euphoria longan*, *Hibiscus tiliaceus*, *Jasminium mesnyi*, *Litsea monopetala*, *Murraya paniculata*, and *Pittosporum tobira*. This insect is very common in lychee fruit tree orchards near Shenzhen in the Guangdong region of China. Easton (1992) reported it from the Seac Pai Van Agricultural Park in Macau. Its distribution also includes the Hainan, Hunan, Guizhou, Guangxi, and Yunnan provinces of China, Japan (Peng and Liu 1992) as well as Hong Kong (Lee and Winney 1981).

Seliza lignaria (Walker). 9 May 1997, ERE leg, NEW RECORD, Taipa Island, Macao, ex. *Miscanthus* grass along hiking trail in recently burned vegetation. Fennah (1956) listed it from Hong Kong and the Guangdong province of China, and it is also believed to occur in the Anhui, Fujian, Guizhou, Hunan, Sichuan, Yunnan, and Zhejiang provinces of China and India (Peng and Liu 1992).

Medler (1992) reported *Salurnis marginella* (Guérin-Meneville) and *Geisha distinctissima* (Walker) as occuring in Macao in the early part of this century, but we have been unable to document their presence in this study.

Fulgoridae

Fulgora candelaria (L.), lantern fly or lantern bug. 2 May 1994, Cheong Pak Fai leg, Coloane Island; 10 Dec 1990, ERE leg, Guia Hill near lighthouse, Macao Peninsula, ex. *Litchi chinensis*, *Euphoria longan*, *Morus alba*, *Sapium sebiferum*. Kershaw

and Kirkaldy (1910) were probably the first to describe, illustrate, and discuss the life history stages in the area known as South China which includes Hong Kong and Macao. Even though four host plants are given above, Kershaw and Kirkaldy (1910) felt that *E. longan* and mango trees were the most important for the reproduction of this species. Its distribution also includes India (Assam), Cambodia and the Hainan, Hunan, Guangdong, Guangxi, and Sichuan provinces of China.

Zanna chinensis (Distant). 31 Aug 1990, ERE leg, Taipa Island, Macao, ex. *Casuarina equisetifolia*, horsetail tree. There are also records of this species in Hong Kong from the Tai Lung Farm insect collection. Wu (1935) recorded it from the Naga Hills area between India and Myanmar (Burma).

Margarodidae

Icerya purchasi Maskell, cottony cushion scale. 10 Feb 1994, PWW leg, Coloane Island; 12 May 1997, ERE leg, Taipa Island, NEW RECORD, ex. *Cassia surattensis*, the sunshine tree, *Acacia confusa*, *Acalypha wilkesiana*, *Casuarina equisetifolia*, *Hypericum chinense*, Chinese St. Johnswort, and *Pentas lanceolata*. In Hong Kong, Lee and Winney (1981) reported this species from *Rosa* spp. and *Citrus limonia*, Chinese lemon. It has a widespread distribution including Japan, Korea, Philippines, Indonesia, Malaysia, and Sri Lanka in southeastern Asia, including the Gansu, Guizhou, Heilongjiang, Hunan, Ningxia, Qinghai, and Xinjiang provinces of China (Peng and Liu 1992).

Pseudococcidae

Maconellicoccus hirsutus (Green), Asian hibiscus mealybug. 16 June 1988, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Hibiscus rosa-sinensis*. In Hong Kong, it has been reported from Cuban bast, *H. tiliaceus*. Williams (1996) listed it from Bangladesh, Brunnei, Myanmar (Burma), Cambodia, India, Indonesia, Laos, Malaysia, Nepal, Pakistan, Philippines, Sri Lanka, Thailand, and China in southeastern Asia.

Psyllidae

Macrohomotoma striata Crawford, fig shoot psyllid. 29 Dec 1993, PWW leg, NEW RECORD, Coloane Island, Macao, ex. *Ficus microcarpa* and *Ficus retusa*. In Hong Kong, Hill and Cheung (1978) described small waxy colonies inhabiting apical and lateral shoots of twigs and branches. Hollis and Broomfield (1989) reported it from India and Hodkinson, (1986) listed it from Ryukyu Is.

In the family Tropiduchidae Lee and Winney (1981) reported *Kallitaxila macaoana* (Muir) in Hong Kong, but we have not collected it in this study even though the original type locality was in Macao (Muir 1913).

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BIOLOGY OF *ANDRENA* (*SCRAPTEROPSIS*) *FENNINGERI* VIERECK (HYMENOPTERA: ANDRENIDAE), HARBINGER OF SPRING

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Abstract.—Andrena fenningeri Viereck is the first native bee species to fly each spring at Beltsville, MD; males appear as early as February 9, sometimes before their floral hosts begin to bloom. A permanent aggregation of nests in red clay was studied for 10 years. These univoltine, solitary bees break diapause and move at 4°C from their natal cells toward the soil surface in midwinter, ready to emerge and mate as soon as the topmost soil warms. They thermoregulate by aggregating their nests in the warmest available microclimate, and by basking on cold, sunny days to achieve the minimum 11°C required for flight. The most important host is *Acer rubrum*; *Prunus, Pyrus,* and *Salix* are also visited. Male swarming behavior, phenology, nest structure, and associates (including 5 *Nomada* spp., *Myopa* sp., and the behavior of 3 unusual species of *Eustalomyia* [Anthomyiidae]) are discussed. This bee may be manageable as an orchard pollinator, if suitable microhabitat and supplemental hosts are provided.

Key Words: bees, nests, thermoregulation, phenology, fruit pollination, *Eustalomyia,* conopids, *Acer*

The Holarctic bee genus *Andrena* includes about 700 Eurasian and 500 North American species; both species and individuals are dominant components of the bee fauna during springtime; they are important pollinators of crops and wild plants (see references in Batra 1990). The behavior and ecology of few species have been studied. Most species of *Andrena* are solitary, univoltine, polylectic bees; many of them share hosts, geographic ranges, and times of adult activity; the reasons why there are so many species of *Andrena* remain unknown.

This report concerns the nesting behavior of an Eastern, cold-adapted, polylectic, solitary species, which is the first native bee species to fly each spring at the Beltsville Agricultural Research Center (Prince George's Co., Maryland). Adult activity often begins while snow and ice remain on the frozen ground in shady places, and no plants are yet in bloom. *Andrena fenningeri* Viereck (det. W. E. LaBerge) is in the North American subgenus *Scrapteropsis,* which includes 18 vernal species (LaBerge 1971). The nesting behavior of only one of them, *A.* (*Scrapteropsis*) *alleghaniensis* Viereck, has previously been studied (Batra 1990). This solitary bee resembles *A. fenningeri* in its preference for *Acer* as a nectar and pollen source and in the location of its nest aggregation so as to maximize insolation.

I investigated the behavior of *A. fenningeri* at intervals over a period of 10 years (1987 to 1997), at an aggregation of nests in a sunny spot at the north edge of a large field (the "Rose Garden," off Entomology Rd.). Aggregations of nests of *Andrena* may persist for decades (Chambers 1968, Schönitzer and Klinksik 1990, 1992, Rid-

dick 1992). If the factors that permit or encourage permanent aggregations could be determined, this basic information may prove useful in conserving existing natural aggregations, and also for actively managing *Andrena* bees to pollinate fruit crops. For these reasons, the unusually early adult activity of *A. fenningeri* was investigated.

Materials and Methods

I made observations early in each season and during fair weather, when bees were flying. A total of 214 hours were spent, most of them during the unusually warm and early spring of 1990 (76 hours), and the cool, late spring of 1992 (60 hours). Entrances to nests with tumuli were marked with small, numbered aluminum tags, inserted 2 cm north of each nest. Meteorological data were recorded during visits. Soil temperatures at sites 1–6 were taken by inserting calibrated bimetallic dial probe thermometers to the appropriate depths. Nests were excavated by shovel and trowel after pouring plaster into them, which rendered tunnels easily visible. Adult bees and cleptoparasites were netted, then pinned, or preserved in FAA for dissection under a microscope. Pollen was stained with lactophenol-cotton blue and examined microscopically. I indicate means after ranges (in parentheses). Voucher specimens will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Nests and their Contents

The nests of *A. fenningeri* in level ground (Fig. 1) were vertical tunnels that penetrated the uppermost humus-and-root-filled zone of the clay soil, to a zone of dense, poorly drained, red marine clay, where the cells were made. Nests ended at the top of a zone of gritty "hardpan." From late fall through early spring, the red clay was very moist, often muddy; after the tree canopy had leafed out in May (after adult bees ceased activity), the upper part of the clay dried to an adobe-like, hard consistency (soil penetrometer reading 3.5–4.5 kg/cm), providing protection to the growing brood and dormant adults in the cells. Evaporation and transpiration by plants during the hot and relatively dry summer months dried the clay. Rainy, cool weather, and the cessation of most transpiration after November permitted the soil to moisten and soften. Adult bees emerged from their cells in the softened soil, and crawled toward the surface of the soil during mid-winter. They waited just below the soil surface by late winter, ready to fly during the first warm days of spring.

A total of 22 entire nests was examined (5 in 1987; 3 in 1989; 14 in 1991). Because the lateral tunnels that led to cells were backfilled by the solitary mother bees with soil and obliterated after oviposition, many cells that were found could not be traced to their nests' tunnels (Fig. 1) The nests' tunnels reached depths of 16–25 (20.8) cm, and were 4.5–5.5 mm in diameter. Nest entrances were irregular, 3.5–5.5 mm in diameter, and when new, surrounded by a usually circular tumulus of loose, dry, soil particles 2.0–5.0 (3.3) cm in diameter and 0.5–1.0 cm high. The tumulus may not be rebuilt when it had disappeared due to rain. Nest entrances were often closed by loose soil particles when the bees were not foraging. The entrances to about 20% of the nests, which had been initiated beneath fallen leaves or in dense turf grasses, were difficult to find.

Nests had up to 5 brood cells (1.5) each. They were at the ends of lateral tunnels, which were 1.0–6.0 (2.5) cm long and 3.5–5.0 mm in diameter. Cells were made at depths of 13.0–26.0 (21.4) cm. The 39 cells were nearly horizontal, of the usual ovoid shape of *Andrena* cells, and coated internally with thin, shining, transparent waterproof linings, secreted by Dufour's glands. Cells were 10.0–12.5 (11.0) mm long, 5.0–6.0 (5.5) mm in maximum diameter, tapering to the cell's entrance, which was 2.5–4.0 (3.3) mm in diameter. After oviposition, this entrance was sealed with compressed

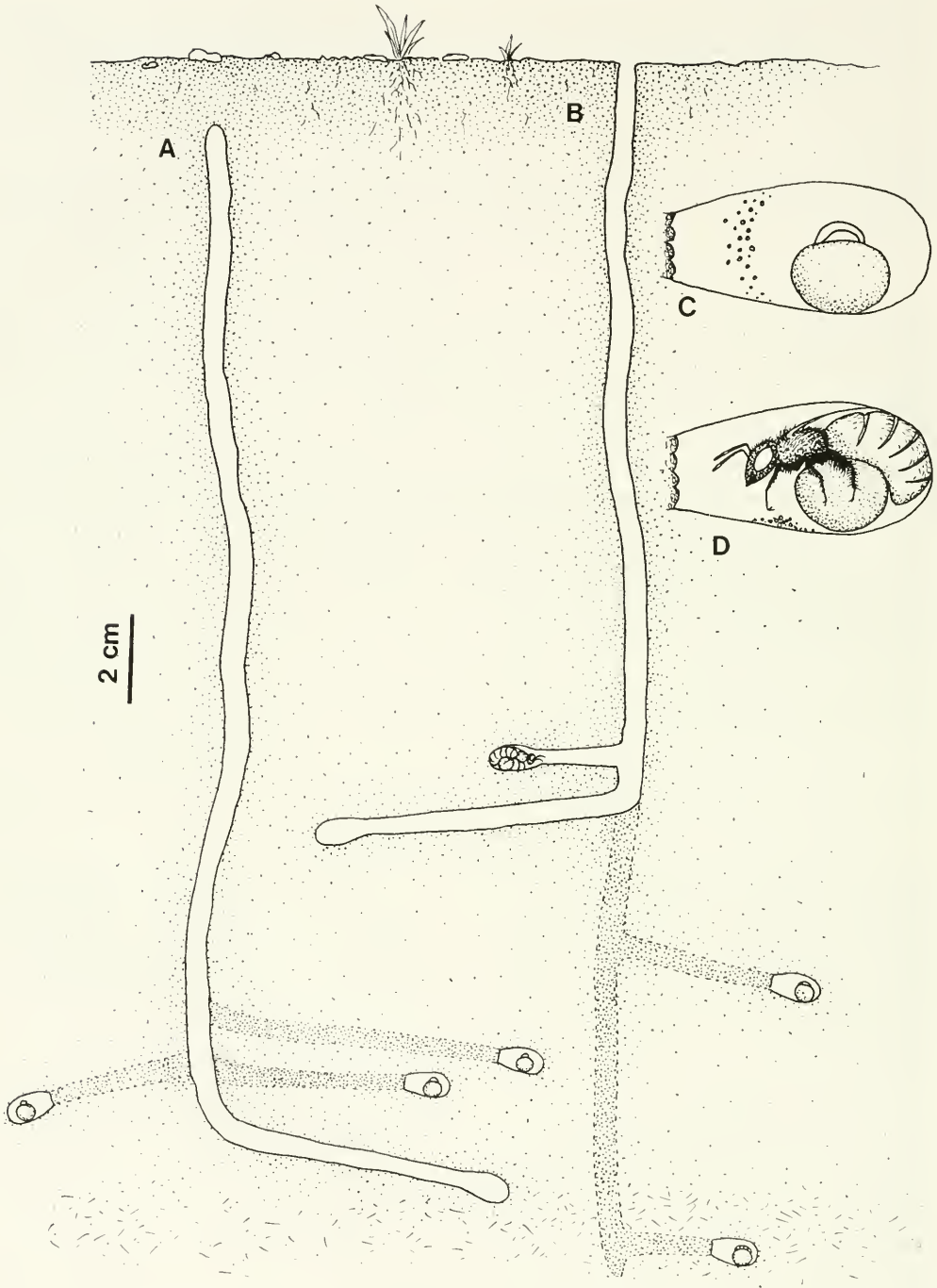

Fig. 1. Two nests of *A. fenningeri* in red marine clay soil(stippled area). Nests extended to a zone of denser soil (hardpan, hatched area), at a depth of 23 cm. The lateral tunnels that led to completed cells were filled with soil by the mother bees. Nest A, closed at the surface, was without an adult bee. It had 3 cells with eggs on pollen balls (examined May 4, 1989). Nest B was open, but without a tumulus. Two sealed cells contained eggs on pollen balls; one of these cells (C) had droplets of moisture on its thin, smooth waterproof lining. Another, open cell (D) had a dead female bee with a large, live conopid maggot filling her abdomen. She died in the position taken by bees when they oviposit (nest examined May 7, 1987).

soil pellets, laid down in two concentric rings around a central depression. The Dufour's-gland secretion in many genera of bees varies in composition. It polymerizes, forming a thin, smooth solid that waterproofs subterranean cells; it can also function as a pheromone, and as food for larvae. In *Andrena,* it is composed mainly of isoprenoid esters (see review in Ayasse et al. 1990).

Small, regularly-spaced, tasteless (to me) droplets, probably of water, were sometimes found on the hydrophobic cell linings, near the entrances of both empty and provisioned cells (Fig. 1C). Perhaps the shape of cells influences the condensation pattern, keeping water from condensing on the hygroscopic provisions, where it would permit spoilage. Yeasts in nectar and ambient fungi ferment and spoil the wetted provisions of many subterranean-nesting bees, causing significant mortality of their larvae (Batra 1970). The soil that seals entrances to cells and laterals of *A. fenningeri* is without a visibly water-repellent lining. It is porous, permitting some circulation of the water-saturated subsoil air. The survival of this bee, living inside cells for many months, and the preservation of its hygroscopic provisions inside humid cells, may depend on such a condensation-site-controlling feature of its brood cells.

Pollen balls (provisions) of *A. fenningeri* that had been made in early spring were olive-green, and composed solely of pollen of *Acer rubrum* L., mixed with nectar. Those made after *Acer* bloom were various shades of yellow, and made of up to 3 species of pollen. Pollen balls were firm, smooth, spheroid, somewhat flat on top, and 3.7–4.0 mm high and 4.0–4.8 mm wide (Fig. 1C). Occasionally, laterals and cells with large pollen balls, but no eggs or larvae, had been filled with earth. Eggs were strongly arched, white, 2.0–2.7 mm long and 0.5 mm thick. Larvae, ranging from 2.5–4.0 mm long, fed on top of the provisions; they later lay on their backs beneath their pollen balls, and reached 8 mm long when all their provisions had been eaten. Larvae transformed to prepupae in late May, after defecation. No cocoons were made. The times of pupation and transformation to adults were not studied.

The time of adult emergence each spring, foraging, oviposition, and larval development varied with weather conditions each year. Although individual females were not marked, many of their nests had been. The appearance of new tumuli late in spring where there had been no nests, the mid-season closure of nests that had been tagged in early spring, and the few cells per nest, indicated that some female *A. fenningeri* make more than one nest each, as do some other species of *Andrena.* At the end of the nesting season, during the first week of May, the old females became disoriented and exhibited displacement activity, such as random digging, as is seen in *Andrena nycthemera* Imhoff (Schönitzer and Klinksik 1990).

Floral Hosts

Andrena fenningeri is polylectic (La Berge 1971, Hurd 1979), visiting *Acer, Prunus, Pyrus, Salix,* and several other hosts. The first host to bloom each spring and the first to be visited for nectar and pollen at Beltsville was *Acer rubrum.* This is a dominant tree, occupying about 20% of the forest canopy near the nests. It is an important food resource for a wide variety of insects, available just as the insects emerge from hibernation (Batra 1985). The first provisions made by *A. fenningeri* were composed of the olive-green pollen from *A. rubrum.* In this respect, *A. fenningeri* resembles a related species, *A. (Scrapteropsis) alleghaniensis* Viereck, which provisions its cells with maple pollen in New York (Batra 1990). Several species of maple trees provide nectar and pollen for various other *Andrena* bees in Europe (Chambers 1968) and North America (LaBerge 1971; more references in Batra 1990). After the red maples finished blooming, *A. fenningeri* visited flowers of *Prunus, Pyrus*

and forbs, growing near the aggregation. Thus, the provisions that were made later in spring were yellow.

The time of emergence of adult *A. fenningeri* in some years coincided with the beginning of bloom of *A. rubrum* and *Salix* sp. In other years, the bees emerged a few days before any host plants had started to bloom. They mated, and began nesting, without having eaten anything. For example, 2 of 3 females that were starting to excavate nests on February 28, 1992, were inseminated, but all 3 had empty crops; 14 of 15 males in a mating swarm on that day had empty crops (one had eaten some maple pollen); all of these 18 early bees had large fat bodies in their abdomens (metasomas) that fueled their flights. By March 2, 1992, 5 males in a mating swarm had empty crops and small fat bodies; 7 females collected while flying over the aggregation still had large fat bodies, but they also had filled their crops exclusively with *A. rubrum* pollen, and eggs were developing in their ovaries. The beginning of flowering by *A. rubrum* varies by up to 2 months with weather conditions in early spring; it begins with male flowers and ends about 2–3 weeks later, with female flowers, the trees being usually dioecious and dichogamous. Bloom began on the following dates at Beltsville: April 2, 1978; March 19, 1982; March 6, 1983 (Batra 1985); February 1, 1989; February 12, 1990; February 21, 1991; February 28, 1992; March 24, 1993 and March 13, 1994.

Thermoregulation by Aggregation

Andrena fenningeri is unusual in its use of dense red clay as a nesting substrate, thus resembling *A. macra* (Riddick 1990, 1992). It nested in clay, even though a large area of exposed, sunlit sandy soil was within about 100 m. Most species of *Andrena* nest in more porous, well-drained soils, especially sand (Miliczky and Osgood 1995, Batra 1990); hence they are called "Sandbienen" in German (Gebhardt and Rohr 1987).

On April 21, 1987, when I discovered the aggregation, nests occupied an area of 5 × 8 m. Most nests (53, with tumuli) were in a 3 × 3 m area with exposed soil; it was a buck (deer) scrape, which was renewed every autumn (Fig. 2, site 1). There were 18 nests/m^2, with a minimum internest distance of 1.0 cm. In the part of the aggregation that was in soil covered with short turf (site 2), nests were fewer, spaced up to 1 m apart. On March 8, 1990, the aggregation measured 5 × 34 m; there were up to 54 nests/m^2 in exposed soil (site 1), with internest distances of 4–18 cm ($\bar{x}$ 9.5 cm; N 31). In the turf (site 2), nests were 1–4 m apart. On March 5, 1992, the aggregation measured 2 × 25 m; there were 100 nests/m^2 at site 1 and 30 nests/m^2 at site 2. The aggregation had about 2,900 nests in 1992. By March 1997, the 2 small pine trees near the aggregation had grown, shading it. the bees had moved most nests 2–3 m to the west, where it was sunnier. The winters and early springs of 1997 and 1998 were unusually rainy. Fewer than 100 nests of *A. fenningeri* remained at site 1 by late March, 1998 (1 nest/m^2 maximum density).

Andrena fenningeri nested in the dense aggregation in only one small part of the large field (Fig. 2, Sites 1 and 2). Aggregated nesting by solitary bees and wasps is common, and some aggregations may persist at a site for over 50 years. There are several, nonexclusive explanations for this phenomenon, including substrate limitation; improved efficiency in foraging; protection from predators and parasites; attraction to others of the same species; an opportunity to save time and energy by re-using existing nests; and philopatry, or re-nesting near the insects' natal nests (see review in Rosenheim 1990). Because *A. fenningeri* was active during early spring when the weather was often cold and rainy, the location of its aggregation in the warmest and sunniest part of the field appeared to be most advantageous; this maximized the number of hours available to the bees for foraging and reproduction. Floral resources were abun-

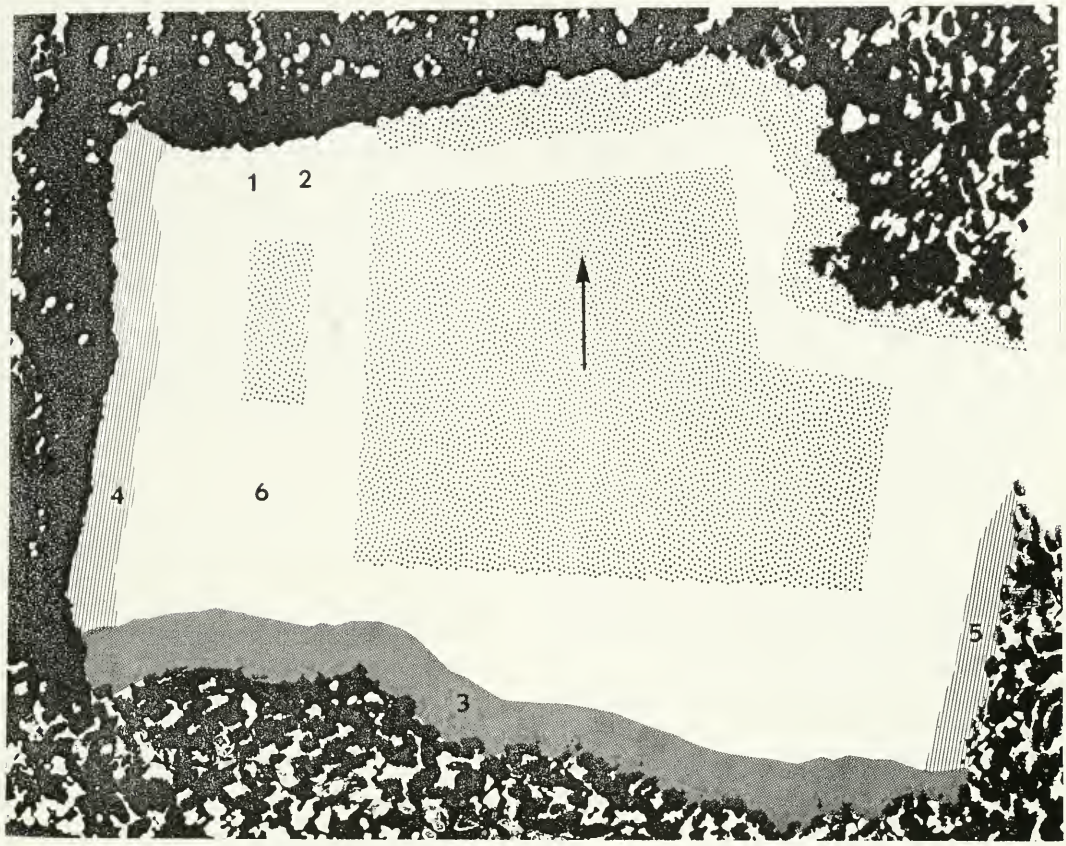

Fig. 2. Field where *A. fenningeri* nested (drawn from aerial photograph). It is 230 m wide, and the arrow points North. Regularly mowed areas of short turf lawn are white (if sunny), striped (if partly shaded) or hatched (if always shaded). Stippled areas indicate locations without nests, being boggy, or fenced and shaded by dense tall grass and shrubs. Temperatures were recorded at locations (Sites) 1–6, all in red marine clay. The main portion of the nest aggregation was in a sunny patch of bare soil at Site 1, and it extended into turf-covered soil (Site 2). There were no nests below the short turf at Sites 3–6; Site 3 was shaded all day; Sites 4 and 5 were shaded in afternoons and mornings respectively; and Site 6 was sunlit all day.

dant, thus not a limitation. The aggregation may have begun decades ago, when a mated founding female successfully nested there, and her descendants returned to the area for nesting (philopatry). Because a closely related, cold-adapted species, *A.* (*Scrapteropsis*) *alleghaniensis,* placed its aggregation of nests in a southeasterly-facing, sandy slope where they received maximum insolation and warmth in early spring (Batra 1990), *A. fenningeri* was suspected of doing likewise, even though its aggregation was in level clay soil rather than in a sandy slope.

In order to test this hypothesis, I made a series of temperature measurements at four depths (2, 8, 15, and 30 cm) at six sites (Sites 1–6, Fig. 2), using bimetallic-dial-probe thermometers. Most of the nest aggregation was at Site 1 (in exposed soil); some nests were in Site 2 (soil covered with short turf).

A split-plot analysis was used on this experiment. The six sites were specifically selected for their shading and vegetation coverage conditions, and are therefore defined as fixed factors in this analysis. The sites are also defined as whole plots of the split-plot design, while the four levels of depth (2, 8, 15, 30 cm) at each site are the sub-

Table 1. Means and Standard Errors for the factorial combination of 4 depths and 6 sites.

Depth	2		8		15		30		
Site	Mean[b]	SEM	Mean[b]	SEM	Mean[b]	SEM	Mean[b]	SEM	Mean[c]
1	11.8	0.77	8.8	0.65	6.7	0.63	5.7	0.56	8.3[c]
2	10.0	0.88	8.7	0.73	8.3	0.71	7.4*	0.62	8.6[c]
3	2.5**	0.82	2.7**	0.68	2.6**	0.66	2.7**	0.59	2.6[c]
4	8.1**	0.89	6.7*	0.73	6.7	0.71	6.1	0.63	6.9[c]
5	8.2**	0.89	6.9*	0.73	6.1	0.71	5.1	0.63	6.6[c]
6	9.9	0.88	7.8	0.73	7.0	0.71	6.7	0.62	7.8[c]
	8.4[d]		6.9[d]		6.2[d]		5.6[d]		

[a] A least-squares-mean test examined possible difference between Site-1 (the one with the greatest nest concentration) means and those of the other five sites. Within a column, a least-squares mean with one asterisk is significantly different from Site 1's mean at $0.01 \leq P \geq 0.05$. A mean with two asterisks is significantly different from Site 1's mean at $P < 0.01$.

[b] Least-square mean.

[c] Mean of all temperature measurements for each site for all four depths.

[d] Mean of all temperature measurements for each depth for all six sites.

plot levels. Measurements of temperature done on different days were defined as haphazard (a random number table was not used). Data were recorded during early afternoon on 7 days from March 3 to March 26, 1992, during the time of peak nesting activity, and used as replication in the analysis. A mixed-model analysis of variance was used to determine the fixed effects of site, depth, and their interaction. A heterogeneous first-order autoregressive covariance structure was included in the ANOVA model to account for the possible associations among depths. Least-significance difference tests ($\partial = 0.05$) were used to compare means of the fixed effects. Results are summarized in Table 1.

Site 1 (the aggregation) was significantly warmer than site 3 at all depths (Table 1). It was warmer than Sites 4 and 5 at depths of 2 and 8 cm, but did not differ from them at 15 and 30 cm. Site 1 did not differ from Sites 2 and 6 at depths of 2, 8 and 15 cm, but, at 30 cm, it was slightly cooler than Site 2, and did not differ from Site 6. The right column of the Table shows the means of all measurements combined from the 4 depths at each site. It shows that the portion of the aggregation at Site 2 was slightly (but not significantly) warmer than the major portion in Site 1, and both of these parts of the aggregation were considerably warmer than areas where the bees did not nest, especially Site 3.

The soil-temperature analysis indicates that *A. fenningeri* used the warmest local area for the aggregation. Thus, the bees thermoregulated by choosing a warm nesting site (and also individually, by basking). Sites 1 and 2 are at the southern edge of a pine-oak forest. The level ground receives maximum insolation at such a location in March (Kimball and Hand 1922, Geiger 1965). The aggregation also benefitted from radiation that was reflected to it from nearby oak tree trunks (see Geiger 1965). Pine trees within the forest broke the cold northwest wind that prevailed on clear, sunny days in Maryland, and they retained heat that was radiated from the soil at night. The protective influence of a forest windbreak to the north of a field edge can raise air temperatures 5 cm above the ground all year, by 11°C above air temperatures in a field near the forest along the opposite, south edge (Wales 1972). Such microclimatic differences are significant; for example, 6 species of vernal wild flowers on a south-facing slope bloomed on average 6 days earlier than the same species growing on a north-facing slope 50 m away; this difference, correlated with cumulative differences in air and soil temperatures, is equivalent to 176 km in latitude (Jackson 1966).

There were slight differences within the aggregation between Sites 1 (exposed soil surface) and 2 (turf covered) that were not statistically significant, but could be detected behaviorally when the temperature in the upper 2 cm of soil was near 11°C (marginal for flight initiation). For example, at noon on March 17, 1992, a sunny day after a frosty night, no bees were flying at either Site 1 or Site 2. At Site 1, temperatures were 11°C at 2 cm, 6.5°C at 8 cm, 4.5°C at 15 cm, and 4.0°C at 30 cm depth. At 15: 30, bees were flying at Site 1 but were not flying at Site 2. At Site 1, soil temperatures by then were 13°C at 2 cm, 10.5°C at 8 cm, 8.0°C at 15 cm and 5.5°C at 30 cm depth. Temperatures then at Site 2 were too cool for flight, being only 10.5°C at 2 cm, 10.0°C at 8 cm, 9.5°C at 15 cm and 6.5°C at 30 cm depth. Although Site 2 was warmer than Site 1 at 15 and 30 cm, it was cooler at 8 cm, and much (2.5°C) cooler at 2 cm depth, where bees usually wait to warm up, before flying. A similar pattern was seen at 13:00 on March 25, 1992, a day of hazy sun after a frosty night: bees were flying at Site 1 but not at Site 2 (Site 1: 14.5°C at 2 cm, 9.0°C at 8 cm, 6.0°C at 15 cm, and 5.5°C at 30 cm depth; Site 2: 11.0°C at 2 cm, 10.5°C at 8 cm, 8.5°C at 15 cm, and 7.5°C at 30 cm). Thus, the sun warmed the upper layers of bare soil at Site 1 more quickly than the same depths in turf-shaded Site 2, permitting flight from Site 1 on cool, sunny days. The insulating turf retained warmth overnight in the lower layers at Site 2, but this did not promote flight activity. Even such slight differences between sites in bare soil and those in turf may be significant for survival among bees that must fly to forage during inclement weather.

Andrena nycthemera also begins adult activity when the soil thaws (as early as February 23 in 1990). Many more bees nested in a sunny part of the aggregation than in a shaded portion, where the soil remained frozen longer, and bees in sunlit areas began seasonal activity several days before those that nested in shady portions of the aggregation areas (Schönitzer and Klinksik 1990). Slight microclimatic differences also influence the nesting behvior of halictine bees (Batra 1997, Potts and Willmer 1997).

Thermoregulation by Individuals

Species of *Andrena* that were investigated by Stone and Willmer (1989) produce relatively little endothermic heat, compared to some other genera of bees; instead they depend on insolation and warmth from substrates to generate the minimum 8–12°C ambient temperature needed to begin flight. Many species of *Andrena* bask at nest entrances and on vegetation before takeoff on sunny, cool days. They include *A. fulva* Müller (Paxton 1991), *A. erigeniae* Robt., which basks on fallen leaves that are 6–9°C warmer than ambient temperatures (Barrows 1978), and *A. nycthemera,* which can begin flights after basking at 8–10°C on sunny days, but cannot fly on cloudy days until the ambient temperature reaches 15°C (Schönitzer and Klinksik 1990). Herrera (1995) found that *A. bicolor* F. foraged on sunny days with an air temperature of at least 12–13°C; these small bees bask in warm microclimates to achieve the minimum internal thoracic temperature of 22°C needed to begin flight.

Both sexes of *A. fenningeri* were able to begin flight on sunny days when the ambient temperature of their microclimate was at least 11°C. Bees were often seen basking just inside nest entrances, on tumuli, beneath or on fallen leaves, and on vegetation. The nearly black bodies of both sexes of *A. fenningeri* bear pale hairs, which are densest over the thorax (where warm-up of flight muscles is needed). In this way, the bees resemble the "heat-trap" structures of pussy willow flowers, which have been shown by Krog (1955) to absorb shortwave light (solar radiation), which passes through pale hairs into their black surfaces, and there becomes long wave radiation (heat), which is trapped in the dead airspace among the pale hairs.

Although *A. fenningeri* required a minimum, insolated temperature of 11°C to begin flying, they were active inside their nests at much lower temperatures. On January 11, 1990, the soil at the aggregation (Site 1) had thawed after an unusually cold December 1989 (−20°C air temperature for several days, freezing the soil). I excavated twenty-seven cells on January 11, to study the phenology of the bees and determine how they can emerge so early each spring. The air temperature (at 1 m, in shade) was 10°C, and soil temperatures were 6°C at 2 cm, and 4°C at 10, 21 and 30 cm depths. Some bees had already emerged from their cells (4 ♂ and 3 ♀); 9 males and 11 females were still in their cells (sex ratio near 1:1). Those in cells were resting on their backs. Bees that had emerged stood upright and had dug as far as 2 cm toward the surface; the earth that they had excavated was pushed backward, and packed into their natal brood cells, covering the fecal layer that had been deposited before their transformation to prepupae late the previous May. When these cold (4°C) bees were disturbed, they vibrated their wings; when they were warmed slightly, they stood upright and began to walk. These bees were stored in tissue culture wells at 4°C for 4 days. Some of them defecated (pale meconium), others chewed on moist soil that was placed in the wells with them. Thus, they were active at low temperatures.

At the aggregation, air temperatures were above normal for January 1990, and by the 18th, the air temperature at 14:00 E.S.T. (1 m, shade) was 16°C, and soil temperatures were 13°C at 2 cm, 12°C at 10 cm (both above flight threshold), 10°C at 21 cm, and 8°C at 30 cm. During January, the bees worked their way toward the surface, and the first bees (males) were flying on February 9, a sunny day, when the air temperature at 14:00 (at 1 m, in shade) was 17°C, and soil temperatures at Site 1 were 11.5°C at 2 cm, 10°C at 10 cm, 8.5°C at 21 cm and 7.5°C at 30 cm. *Acer rubrum, Draba* and *Salix* had just begun to bloom (Fig. 3).

These early males flew slowly, about 2–7 cm above the aggregation (Site 1 only), frequently stopping to bask on dead oak leaves on the ground. Flying males dropped to the ground when clouds obscured the sun and when disturbed by the observer; they could then be captured by hand. On February 12, more nests were examined. One female had partly emerged from her cell at a depth of 17 cm, 3 others had emerged, and were in the soil at depths of 3, 9, and 11 cm, having moved toward the surface. No males remained in their cells; 2 were found in the soil at 3 and 6 cm depths. Soil temperatures were 11°C at 2 cm, 8°C at 20 cm and 6°C at 20 and 30 cm. Only males were seen again the next afternoon (sunny, 15°C), circling low over the aggregation in calm air, but they settled on the ground and crawled around when gusts of wind or clouds arrived. The males made intermittent circular flights over small areas (20–30 cm radius), which gradually moved across the aggregation. No territoriality or male aggression was seen, and the males were not seen in nearby trees, where they formed mating swarms later in February. Female *A. fenningeri* released a pungent citrus odor from their mandibular glands when handled, but males had little odor. Possibly the patrolling males can smell the mandibular gland pheromone, released as the females dig their way toward the surface.

On February 28, 1991, male behavior was similar. Fresh tumuli indicated that some females had begun nesting, but none were flying. Many males were patrolling near the ground in a zigzag pattern, often entering and leaving nests. When shaded, they dropped to the ground, and could be picked up by hand; they could not fly even though they buzzed vigorously, an activity that should warm their flight muscles. They were able to resume flight when replaced in the sun for about a minute. These small males could warm up in the sun at marginal temperatures more quickly than could the larger females, which may explain the absence of flying females. The air temperature

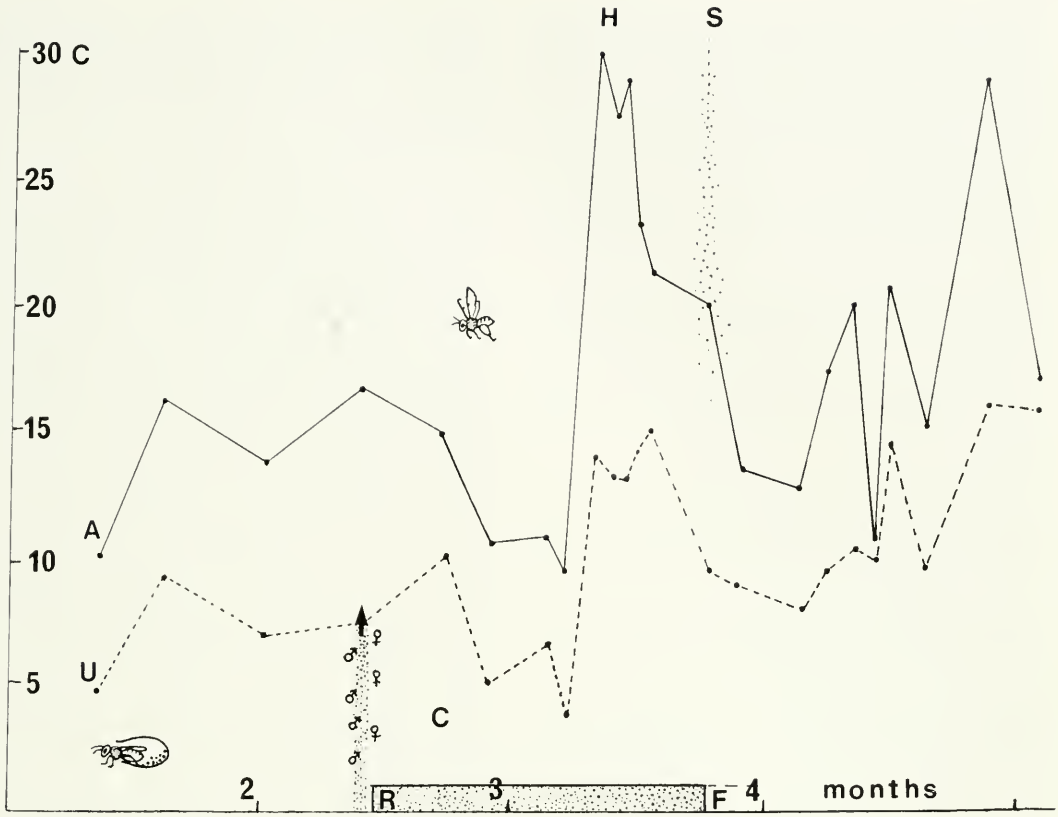

Fig. 3. Temperatures at the nest aggregation (Site 1) and phenology of *A. fenningeri* from January 11 through May 1, 1990, a warmer than normal spring. A, air temperatures at 1 m height in shade; U, underground soil temperatures at a depth of 30 cm. Bees began emerging from brood cells in January; then crawled up the tunnels of their natal nests in early February. Red maples (R bar) bloomed from February 9 to March 21. The first bees (males) emerged February 9; female bees began collecting pollen from red maple by February 22; when maples finished blooming, bee activity declined and females switched to other pollen sources, including fruit trees (F). By May 4, the forest canopy had leafed out, the clay soil at the aggregation had dried and hardened, and only a few senile bees remained. From March 6–15, a record heat wave, with southwest winds, prevailed (H), and the bees were unusually active; on March 16, a cold front brought rain, and snow (S) fell on March 20 and on March 24–25.

(14:30, in shade at 1 m) was 13.5–14.0°C; the soil (Site 1) at 2 cm was 10°C; at 20 cm, 7.5°C and at 30 cm, 7°C. Males that had dropped to the ground to avoid wind often crawled beneath sunlit, dead, dry oak leaves, where temperatures were 12–15°C. In early March, in bright sun, temperatures under sunlit oak leaves reached 22°C when the ambient air temperature was 18°C. In early March 1992, some males that had been flying among trees in the mating swarm basked in the sun on dead leaves, but they crawled under the leaves when the wind gusted or clouds passed; some slept overnight in nest tunnels. When the air temperature at 1 m (shade) on a hazy day was at the 11°C threshold for flight, no female bees flew, but males were able to fly slowly for short distances between bouts of basking in the weak sunlight. On a cloudy day, with air at 11°C, the temperature was only 10°C below a fallen leaf, and also at 2 cm in the soil; insolation was insufficient on cloudy days, thus, no bees flew.

Because *A. fenningeri* made more nests in the portion of the aggregation that was

in bare soil (Site 1) than in the part that was in short (2–4 cm) turf (Site 2), and because bees emerged earlier each spring at Site 1 than at Site 2, soil temperatures at Site 1 were compared with those at Site 2. Although no statistically significant temperature difference between Sites 1 and 2 was detected in March, 1992 (see Table 1), there were small differences between the sites that may have been sufficient to account for the slightly earlier, and slightly more, activity at Site 1, especially early in the spring, when temperatures marginally permitted flight.

Temperatures were measured at Sites 1 and 2 at the same time of day (early afternoon) on 13 days in March and April, 1990 and 1993. Site 2 was cooler than Site 1 by a mean of 2.6°C at 2 cm, and by 1.1°C at 8 cm; Site 2 was warmer than Site 1 by 0.4°C at 15 cm and by 1.4°C at 30 cm depth. Evidently, the upper levels of bare soil (Site 1) warm more rapidly each sunny day than the same levels under grass, but the insulating grass (Site 2) retains warmth at lower levels overnight. The difference between Sites 1 and 2 was most prominent during sunny weather, for example on March 8, 1990, a sunny day after a clear, cold night, at 2 cm depth (where bees wait before flights), Site 1 was 14°C (warm enough for bees to fly), but Site 2 at 2 cm depth was only 10°C, which was below the flight threshold. However, after a several days of rain on a cloudy day, there was little difference between Sites 1 and 2.

The behavior of male *A. fenningeri* in mating swarms was also influenced by microclimate. At first, males flew only a few centimeters above the warm ground, where most nests were aggregated. As the air temperature warmed, many males moved their patrolling to the tips of the branches of small (4–5-m-tall) pine trees near the aggregation, where they formed swarms. On February 28, 1992, males swarmed around the pine trees at an air temperature (1 m, shade) of 17.5°C. When clouds or haze arrived, the males suddenly ceased flying, alighted, and crawled between the dark green pine needles (which would retain heat); they resumed their flights when the sun reappeared.

Behavior of Males

The behavior of male *Andrena* bees has been described and reviewed by Barrows (1978), Gebbardt and Röhr (1987), and Hallmen (1991). Males may emerge simultaneously with, or earlier than, their females each year. They swarm conspicuously in the sunshine, circling and zigzagging above aggregations of nests, around flowers of host plants, and around tall landmarks, such as selected trees near aggregations. Males of most species are non-territorial, and they jointly patrol in search of females, without noticeable interactions among males. Males of *A. nycthemera* are unusually aggressive, biting each other and competitively digging in the ground, searching for emerging females (Shönitzer and Klinksik 1990). Despite the large numbers of both sexes that emerge and mate within a few days, and the numerous times males are seen pouncing on females and on various small dark objects, actual copulation is surprisingly rarely observed. I also did not observe the mating of *A. fenningeri,* in spite of many hours spent watching their behavior.

Both sexes of *A. fenningeri* produce a lemon-like odor from their mandibular glands when captured. It is most distinct in females. The mandibular gland secretions of some *Andrena* bees contain complex mixtures of spiroacetals, monoterpenes, and other compounds (Bergström and Tengö 1982). The secretion of *A. fenningeri* probably includes geraniol and citronellol, which are major components in other species of *Andrena* (Bergström and Tengö 1982). Male bees use these secretions to mark the areas that they patrol in search of females (Bergström and Tengö 1982, Gebhardt and Röhr 1987, Hallmen 1991); and female bees use both mandibular-gland and Dufour's-gland secretions to mark and iden-

tify their nests (Ayasse et al. 1990; Steinmann 1990).

During an unusually warm spring, the first male *A. fenningeri* emerged on February 9, 1990, before the females. They emerged as late as March 7, in 1993, also before the females appeared. Some years, males flew before any host plants bloomed; in other years, the first bees appeared when hosts started blooming. *Andrena nycthemera* males also may begin flying before any food is available (Schönitzer and Klinksik 1990). During their first activity, males crawled, or patrolled, flying in the sunshine some 2–8 cm above the bare soil at Site 1, which radiated heat, warming the relatively calm layer of air near the ground. They flew upwind in small circles or in slow, wavering patterns, occasionally waiting on fallen leaves when clouds passed. They also fell to the ground and "froze" when alarmed (by my movements) and could be caught with the fingers. On cool days, newly emerged females also displayed such thanatosis, when disturbed, becoming immobile, dropping to the ground, with legs held stiffly, parallel and close to their bodies, a behavior similar to that of elaterid beetles. Sometimes, such bees relaxed, and slowly crawled beneath dead leaves. This behavior was seen only in early spring, before host plants began to bloom. Perhaps it is an energy-conserving defense mechanism, used at a time when the bees were subsisting on their stores of fat. Male *A. fenningeri* were seen entering and leaving exit holes and nest entrances. Some males slept in holes, but they did not dig for females. Occasionally, both males and females crawled on the surface of the aggregation, but mating was not seen there.

Most females emerged each year after one or more warm, sunny days, and fresh tumuli indicated that nesting had begun. At this time, many male *A. fenningeri* ceased patrolling at the aggregation, and instead, they swarmed among the bare branches of an oak tree and around two small pines (*P. virginiana* Mill.) growing next to the aggregation. Males of both *Nomada sayi* Robt. and *N. perplexa* Cress. swarmed together with the males of *A. fenningeri*, both at the aggregation and around the trees; perhaps they have similar pheromones. Male *A. fenningeri* were seen to emerge from the ground and fly up to join these others around the trees.

Males of *A. fenningeri* patrolled areas around the tips of the pine branches. They zigzagged along the downwind sides of the branches at a height of 2–4 m, occasionally alighting. They flew from one branch tip to the next, briefly hovering while facing the tip of each branch, before flying upwind to the next branch, where they zigzagged toward its tip. This was repeated, until they reached the upwind (and sunny) side of the tree, from which they drifted back on the breeze, to repeat the process of inspecting branch tips. Mating was not observed at these "swarm trees." Similar upwind and zigzag patrolling, alternating with downwind drifting, occurs in *A. vaga* (Hallmen 1991).

On March 2, 1992, an attempt to attract males to females in a swarm was made. Four live females were tied with threads to the tips of pine branches where many males patrolled. They were conspicuous, but were bypassed by 16 males. Another 7 males hovered to briefly inspect them, and 4 males pounced on the females, but immediately released without mating. These females orally released a distinct lemon-like odor. Other bees that were swarming around the pine trees were netted, yielding 10 males and 1 female, indicating that females were also attracted to these "swarm trees" (see Hallmen 1991). The captured female and 5 males were dissected; the female was inseminated and had fed on maple pollen, but the males had not eaten pollen or nectar, their crops being collapsed and their guts empty. A sample of 6 females that were flying over the aggregation on March 2 had all eaten maple pollen, and all were inseminated. Similarly, on February 28, 1992, 14 males that were swarming

around the pine trees were dissected; 12 had empty crops and guts, 1 had eaten nectar, 1 had eaten some maple pollen; and most had large fat bodies. The females that were collected from nests with tumuli on that day varied: 1 had not mated or eaten, and still had rectal meconium; 2 were inseminated but had not eaten. The number of males seen around the swarm trees and above the aggregation each year slowly declined as spring advanced, and a week to 10 days after emergence, males were no longer seen near the aggregation. By this time, host plants were blooming, and the males searched for females there.

Parasites and Associates

As with other species of *Andrena* worldwide, *A. fenningeri* was associated with several other insects at the aggregation. These included the halictine bee, *Dialictus versatus* (Robertson), nesting at the western edge of the aggregation, and its cleptoparasite, *Sphecodes stygius* Robertson. Five species of *Nomada* were active at the *A. fenningeri* aggregation, which I identified as *N. bella* Cresson, *N. cressoni* Robertson, *N. parva* Robertson, *N. perplexa* Cresson and *N. sayi* Robertson. *Nomada perplexa* was by far the most abundant of these cleptoparasitic anthophorid bees. They often entered nests, but I did not find any *Nomada* in brood cells. A conopid fly (probably *Myopa* sp.), bombyliid flies, blue and black fungi in brood cells, and three species in the genus *Eustalomyia* (Anthomyiidae) also were present. These anthomyiids were attracted to flying *A. fenningeri,* but not to *D. versatus,* which had a different, more erratic flight pattern.

The grouping of nests in a perennial aggregation permitted a permanent population of these natural enemies, but the bees had several defenses against them. For example, many nests were initiated beneath dead leaves, which concealed their entrances; tumuli often were not rebuilt when they had been destroyed by rain, which made nest entrances inconspicuous; nest entrances were temporarily sealed with soil particles; returning foragers dodged cleptoparasites that followed them; foragers took circuitous routes, and entered nests abruptly, thus confusing and evading trailing parasitic bees and flies. Such evasive techniques have been seen in other species of solitary bees and wasps (Hager and Kurczewski 1985, Meyer-Holzapfel 1986, Rosenheim 1990, Schönitzer and Klinksik 1990).

The most abundant of all the parasites were three *Eustalomyia* species (det. W. Downes, Jr.). The only hosts previously known for this genus of anthomyiid flies are the solitary crabronine wasps, *Ectemnius paucimaculatus* (Packard) in North America (Krombein 1964), and *E. cavifrons* (Thomson) in Europe (Meyer-Holzapfel 1986). According to Downes (in litt.), the three species that are associated with *A. fenningeri* may be the first to be associated with bees, and probably are new records, because these flies appeared much earlier in spring than those species that are associated with crabronine wasps.

The *Eustalomyia* species appeared in succession; of samples sent for identification, the first (species A, males) being active at the aggregation as early as March 9, 1992, 12 days after the first bees emerged that year. Females of species A were active at the aggregation March 15–22, 1990, and March 25, 1988; species-A males were found as late as April 27, 1988. Females of species B were collected at the aggregation on April 4, 1988, and females of species C were present on April, 27, 1988.

The behavior and gross morphology of all three species of *Eustalomyia* were similar. It was not possible to distinguish among them in the field; thus, they will be discussed collectively here. Initially, they were assumed to be the anthomyiids, *Leucophora obtusa* (Zetterstedt), and *L. marylandica* (Malloch), which are common at aggregations of three species of *Colletes* bees at Beltsville, and behave similarly to *Eustalomyia. Leucophora obtusa* also par-

asitizes *Andrena nycthemera* in Europe (Schönitzer and Klinksik 1990).

Cleptoparasitic anthomyiid and sarcophagid flies are often classified according to their behavior in relation to their hosts. Some are "satellite flies," also called "station takers," which perch near the nests of hosts, abruptly taking flight to pursue returning foragers to their nests. Others are "hole searchers," flying about in search of hosts' nests (Hager and Kurczewski 1985, Wcislo 1986, Meyer-Holzapfel 1986). The host bees and wasps defend their nests against satellite flies by evasive maneuvers in flight. Intense activity by both hosts and parasites at dense aggregations also causes confusion of the parasites. Closure and concealment of nest entrances provide some protection from hole-searching flies and the cleptoparasitic bees, *Nomada* and *Sphecodes* (see review in Rosenheim 1990).

A 1-m^2 area in the densest part of the aggregation (54 nests/m^2 on March 8) was watched for 74 minutes on a warm, sunny day (10:10–11:24, March 15, 1990), in order to observe the activities of cleptoparasites, especially *Eustalomyia.* During this time, *A. fenningeri* foragers left nests 4 times and returned with yellow pollen 10 times (one trip lasted 14 minutes); two bees remained at nest entrances; usually, one *Nomada parva* continually patrolled above the nests; once one alighted briefly, to fan her wings at a nest entrance (probably to bring up odors from the nest).

Most of the time, two *Eustalomyia* were perched in the area. The flies jumped up and briefly followed patrolling *Nomada* twice; they chased each other once; and one briefly followed a falling leaflet. One or two flies 10 times followed *A. fenningeri,* while both leaving and returning to their nests. Flies were seen entering *A. fenningeri* nests 3 times. In one instance, two flies followed a bee returning with pollen; one of them alighted and peered into the nest headfirst, then turned and slowly backed into the nest, until it disappeared. After 4 minutes, it reappeared at the entrance, waited 10 seconds, and flew away (the bee remained inside). Another time, two flies followed a bee returning with pollen (she zigzagged in an attempt to lose them); one fly followed this bee into her nest headfirst, but left within a minute. Once, two flies followed a bee laden with pollen to her nest entrance, which was beneath a fallen leaf. On alighting near the nest, the flies shoved each other for 1–2 seconds, until one of them flew away. The "winner" then slowly backed tailfirst into the nest entrance, rested there for 2 minutes, then backed down into the tunnel, out of sight. After another 4 minutes, the fly's head reappeared at the entrance, the fly walked out of the nest and rested for 2 minutes facing away from it, cleaned itself, and departed.

The bees defended their nests in several ways. The entrances to many nests were closed with plugs of soil or obscured by loose tumuli. Entrances to other nests were camouflaged by, or hidden beneath, dead leaves, grass blades, and twigs. Bees that appeared to be ready to leave their nest entrances on foraging trips were hesitant, backing down when other insects flew nearby; departing bees were briefly followed by flies, but they did not seem to take evasive paths. Ten bees, returning to their nests that were followed by *Eustalomyia,* performed elaborate evasive maneuvers before abruptly diving into their nests' entrances. In contrast, two returning bees that were not followed by flies entered their nests directly. During evasive flights, returning bees pursued by flies zigzagged; one of them left the area for 2 minutes, returning to her nest again without the fly; another bee shook off two closely-following flies when she crawled beneath a leaf to the hidden entrance of her nest; a third bee had nested in the shadow of a large piece of debris; the pursuing fly did not follow her, but alighted in a sunny area nearby. Another bee had nested in turf; this bee hit the grass blades and fell to the ground when she tried to zigzag to evade two pursuing flies. The placement of nests in shadows beneath de-

bris may help prevent *Eustalomyia* attacks, but this may also be disadvantageous because less warmth (insolation) would be present at such shady sites.

Adult *Eustalomyia* spp. first appeared at the aggregation soon after the bees began to emerge. *Nomada perplexa* emerged at the same time as their hosts, and even shared mating aggregation sites with *A. fenningeri*. On cool, sunny days in early spring, *Eustalomyia, Nomada,* and their hosts basked on the warm soil at the aggregation. The initiation of adult activity by these insects in February through March varied by up to a month in different years, but the time of its termination each year in early May varied by only about a week.

Only one small maggot was found (May 4, 1989), although 22 nests of *A. fenningeri* were examined, and *Eustalomyia* were abundant. It was on the side wall of a sealed cell that contained a normal egg on an intact pollen ball, in a marked nest. This nest was closed at the surface, with only this one cell, at the end of a backfilled lateral. This cell was being provisioned on April 21, and *Eustalomyia* had been very active at the aggregation. At that time, this nest had a tumulus; probably it was a new, secondary nest. There was no bee in this closed nest when it was examined on May 4. The genus *Eustalomyia* is ovoviviparous (Meyer-Holzapfel 1986). Those species associated with crabronine wasps oviposit at the host's nest entrances; the fly larvae hatch immediately, and crawl to the wasps' food stores (Meyer-Holzapfel 1986). In contrast, the species that are associated with *A. fenningeri* enter the bee's nests, even while the adult bee is still inside, and they somehow manage to deposit their eggs (or perhaps larvae) inside cells that have been completed, but not yet sealed (the cell plug and long, backfilled lateral would probably prevent these delicate flies and their maggots from entering sealed cells). Because solitary bees immediately begin to seal their brood cells and backfill laterals on completing oviposition, which occurs after a period spent smoothing and perfecting the pollen ball (Batra 1970), it would be difficult for the flies to seize this opportunity. If flies oviposited in cells before pollen balls are completed, the gyrations and grooming of the pollen ball by the bees working in the confinement of their cells would damage fly eggs or larvae, and if detected, the bees may kill, eat, or remove them. On March 22, 1990, one *Eustalomyia* fly that had backed into a nest that was occupied by a bee, as if to oviposit, rapidly emerged while buzzing its wings, agitated, as if it had been attacked by the defensive bee. It then waited, 1 mm from the nest entrance and facing it, for the next 33 minutes. Perhaps the flies deposit their eggs in crevices in open laterals and the hatchling larvae slip into the open cells while the bees are temporarily quiescent, during the process of oviposition.

Conopid flies also parasitize these bees. On May 7, 1987, two dead female *A. fenningeri* were found, one in each of two nests. In both instances, the bee, with swollen abdomen, was poised over a completed pollen ball, as if to begin oviposition (Fig. 1D). One of them contained a brown puparium; a large maggot emerged from the pulsating abdomen of the other bee 30 minutes after her collection. Evidently, the pressure of the maggots inside the bees mimicked the stimulus of eggs that were ready to lay, causing the bees to prepare normal-appearing pollen balls, and take the position for egg laying, as they died (there may have been additional stimuli). Both nests had other cells with eggs on pollen balls, suggesting that these bees had laid eggs soon before the rapidly-growing maggots consumed most of their abdominal contents. According to Smith (1966), *Andrena* bees are usually parasitized by species of conopid flies in the genus *Myopa*; host bees may actively fly and feed with a large maggot nearly filling the abdomen; death of the bee occurs shortly before the maggot's pupation.

Conclusion

Andrena fenningeri is a species of solitary, vernal, univoltine bee that successfully exploits ecological resources that become available as soon as the ground thaws. In order to be prepared for the earliest bloom, this bee nests in permanent aggregations in the warmest available microhabitat. Overwintered adults begin to move out of their natal brood cells toward the surface in midwinter. On emergence from nests, they mate, often before food is available, and soon females begin to excavate new nests in the aggregation. When the temperature is marginal for flight, these black bees bask in the sun, to gain sufficient warmth for their activities.

This species first feeds on early-blooming red maple and willow, but later shifts to pear and peach as they begin to bloom. It may be possible to manage this species for orchard pollination, if suitable nesting sites and early-season hosts are provided. Areas of sunny, exposed, level clay soil along the north edges of orchards could be prepared and kept free of vegetation. They should be backed along their north sides by windbreaks, such as forests, walls, or solid fences. Red maples and willows should grow within 100 m. The initial population of bees could be obtained by transplanting cores of soil that contain nests from an existing aggregation, as is done to move soil-dwelling alkali bees (Batra 1970). Once a population of bees is established near the orchard, it would become permanent and maintenance-free, except for the need to remove (scrape) all vegetation from it each winter to permit maximum insolation in early spring.

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REVISION, CLADISTICS AND BIOGEOGRAPHY OF THE NEOTROPICAL GENUS *SOUZALOPESMYIA* ALBUQUERQUE (DIPTERA: MUSCIDAE)

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Abstract.—*Souzalopesmyia* Albuquerque, a monophyletic Neotropical muscid genus of five species, is reviewed to include two new species, ***Souzalopesmyia paraensis* Carvalho, new species** (Brazil: Pará), and ***Souzalopesmyia sulina* Carvalho, new species** (Paraguay: Canindeyú). Ground plan characters of the Phaoniinae as outgroup were used in a cladistic analysis of the genus. The phylogenetic relationships found are (*S. amazonica* (*S. paraensis* (*S. singularis, S. sulina*)) (*S. carioca*)) and these seem to support at least two biogeographical hypotheses: 1, The basal clade, *S. amazonica,* suggests a date of origin for the genus as far back as the Late Cretaceous; 2, The occurrence of *S. paraensis* in Belém, along south side of the Amazon River, suggests a single dispersal event to colonize that region, in a more recent time, which belongs to the northwestern track.

Resumo.—*Souzalopesmyia* Albuquerque, um gênero monofilético de Muscidae Neotropical com três espécies é revisto para incluir duas novas espécies, ***Souzalopesmyia paraensis* Carvalho** (Brasil: Pará) e ***Souzalopesmyia sulina* Carvalho,** (Paraguay: Canindeyú). Para a análise cladística do gênero, foram utilizados, como grupo de fora, os caracteres do plano básico de Phaoniinae. A partir do relacionamento filogenético encontrado (*S. amazonica* (*S. paraensis* (*S. singularis, S. sulina*)) (*S. carioca*)) podem ser retiradas, no mínimo, duas hipóteses biogeográficas: 1. O clado basal, *S. amazonica,* sugere a data de origem do gênero para o Cretáceo Superior; 2. A ocorrência de *S. paraensis* em Belém, ao sul do Rio Amazonas, sugere que um único evento de dispersão ocorreu para colonizar esta região, em uma época mais recente.

Key Words: Cladistics, biogeography, phylogenetic analysis, *Souzalopesmyia,* taxonomy

Souzalopesmyia Albuquerque 1951 is an unusual genus of rare Neotropical Muscidae because all of its species are yellow. In general, yellow species are inhabitants of very dark shaded habitats. The genus was proposed by Albuquerque (1951: 53) to accommodate two new species, *S. carioca* and S. *amazonica.* Subsequently, Pont (1972) included *Mydaea singularis* Stein 1911, in the genus.

The relationship of *Souzalopesmyia* with other genera of Muscidae is confusing. Malloch (1929) described *Peruvia* (a preoccupied name, now a synonym of *Souzalopesmyia*) to include only *Mydaea singularis* Stein, and considered it to be close to *Charadrella* Wulp 1896 (Cyrtoneurininae). Séguy (1937) synonymized *Peruvia* with *Mydaea* Robineau-Desvoidy 1830 (Mydaeinae), and Albuquerque (1951) considered *Souzalopesmyia* to be close to *Oramydaea* Snyder, the latter being an Afrotropical ge-

nus of Mydaeinae now synonymized with *Myospila* Rondani 1856. Hennig (1965), after examination of the ovipositor of the type species of *Peruvia* put it close to *Helina* Robineau-Desvoidy (Phaoniinae). Carvalho (1989d) included *Souzalopesmyia* in his cladistic analysis of Muscidae and considered it as genus of Phaoniinae (Pont 1972, Carvalho et al. 1993).

The present paper adds two new species to *Souzalopesmyia,* presents a cladogram of the genus, and reflects upon the biogeographic relationships among the included species.

Material and Methods

Specimens from the following institutions were studied for comparative purposes: Department of Zoology, Universidade Federal do Paraná (DZUP), Curitiba, Brazil; Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil; Staatliches Museum für Tierkunde (SMT), Dresden, Germany; Museo Nacional de Historia Natural (MNPA), Asuncion, Paraguay.

The terminology and abbreviations used here are those in McAlpine (1981) and Carvalho (1989a), and the descriptions of the type-specimen labels follows O'Hara (1982).

The sister group of *Souzalopesmyia* is unknown although the genus is considered as one of the most basal members of the tribe Phaoniini (Pont and Carvalho 1997). The sister group may be found in Afrotropical Phaoniini (Pont 1980), which is composed of three genera. Two of these genera, *Phaonia* Robineau-Desvoidy, 1830 and *Helina,* are true but paraphyletic genera of Phaoniini (Hennig 1965). On the other hand, the sister group may be found in a more basal group of Neotropical Muscidae. Character polarities for the genus were based on the ground plan of Phaoniinae, and the assignment by Pont (1986) since no phylogenetic analysis for these genera is available (Huckett and Vockeroth 1987, Carvalho 1989d).

Table 1. Character state distribution among species of *Souzalopesmyia.* 0 = plesiomorphic character states; 1 = apomorphic character states; ? = missing data. Taxonomically useful characters for the species of *Souzalopesmyia.* Characters with an * were used in phylogenetic analysis.

outgroup	000 000 000 000 00
S. amazonica	000 100 010 101 11
S. carioca	101 001 111 101 11
S. paraensis	000 011 110 001 11
S. singularis	000 011 100 111 11
S. sulina	?10 011 100 111 11

*1. Number of frontal setae in female: 0) three; 1) two.
2. Frontal setae in male: 2) two cruciate; 1) two, the lower cruciate, the upper reclinate.
3. Vti: 0) parallel; 1) divergent.
4. Postocular setae row in male: 0) complete and distinct, whole row of setulae reaching epistome; 1) incomplete, row of setulae reaching only to basal half of eyes.
*5. Postocular setae row in male: 0) whole row of setulae black; 1) composed of black and yellow setulae; latter beginning after basal half of eye and reaching epistome, but 1–2 with black setulae.
*6. Number of Dc prst: 0) two; 1) one.
*7. Acr female prst: 0) distinct from the ground setulae; 1) not distinct from the ground setulae.
*8. Proepisternal seta: 0) strong, similar in length to the upper anepisternal setae; 1) weak, less than the length of upper anepisternal.
9. Crossvein dm-cu: 0) almost straight (Albuquerque 1951: Fig. 11); 1) weakly curved (Albuquerque 1951: Fig. 13).
*10. Fifth sternite shape: 0) without sharp depression on posterior side (Fig. 1); 1) with sharp depression on posterior side (Figs. 2, 3, and Albuquerque 1951: Figs. 10 and 12).
*11. Cercal plate: 0) round outline (Fig. 4, and Albuquerque 1951: Fig. 4); 1) squared outline (Figs. 5, 6).
12. Head appearance: 0) not elongate; 1) elongate (Albuquerque 1951: Fig. 1).
13. Number of ocellar setae; 0) two; 1) none.
14. General ground color of the flies: 0) not yellow; 1) yellow.

Table 1 includes all useful characters and character states distribution of *Souzalopesmyia* species and their polarities used in the present paper. The program Hennig86, version 1. 5 (Farris 1988) was used for the phylogenetic analysis, applying the implicit enumeration (ie*) option. Consistency (CI)

and retention (RI) indices were calculated excluding uninformative characters (autapomorphies and synapomorphies of the genus).

Taxonomy

Souzalopesmyia Albuquerque 1951

Peruvia Malloch 1929:104 (preocc. Scudder 1890). Type-species, *Mydaea singularis* Stein, 1911 (orig. desig.).

Souzalopesmyia Albuquerque 1951:53. Type-species, *Souzalopesmyia carioca* Albuquerque, 1951 (orig. desig.).

Diagnosis.—*Souzalopesmyia* may be recognized by its typical head and antenna shape, by the setulose parafacials for half their length, and by the absence of ocellar setae. Also, they are wholly yellow flies except for the presence of stripes on the abdomen (Albuquerque 1951: Figs. 3, 16).

Description.—Male head dichoptic (Albuquerque 1951: Fig. 1), narrower than in female. Frons with orbital setae reclinate, and without crossed setae on frontal vitae. Ocellar setae absent. Antenna long, reaching epistome. Arista plumose, longest hairs equal to greatest antennal diameter. Parafacials setulose on upper half. Female proboscis as in Fig 14. Dc 1–2:3. Acr not distinct from ground setulae, except in female of *S. amazonica*. 2 postpronotals. Ia: 1:2. Sa: 1:2, second weak, about half length of first. 2 pa. 2 subequal npl setae. Pra absent. Disc of notopleuron bare. Anepisternum with a short seta in upper anterior corner. Anepimeron, greater ampulla, vallar ridge, and meron bare. Ktps 1:2 (not 1:1:1 as stated by Albuquerque 1951). Metathoracic spiracle small, triangular, with yellow setulae on margin. Prosternum bare. Fore tibia with 1 PD submedian setae. Fore tarsomere 1 with 1 V setae. Mid femur with 1 AD, 1 D, 1 PD and 1 P preapical setae. Mid tibia with 2–4 P median setae: 1 strong V apical setae. Hind tibia without calcar and with 1 AD median setae, 1 D, 1 AD, 1 AV apical setae. Veins bare, except for costa. Vein M_{1+2} curved slightly toward vein R_{4+5}. Lower calypter of *Phaonia*-type. Sternite 1 bare. Male aedeagus as in Figs. 10–12. Ovipositor long, tergites, sternites and membranes covered with microtrichia (Figs. 15, 16). Three elongate spermathecae. Egg: *Phaonia*-type.

Monophyly.—*Souzalopesmyia* Albuquerque is a monophyletic genus based on the following synapomorphies: 1, Head lateral appearance elongate; 2, Ocellar setae absent; 3, Ground colour yellow.

Remarks.—The species of *Souzalopesmyia* are rare and have similar facies. Based on current collection records, they are found in rainforest habitats. They may be nocturnal, as they are rarely collected by day.

Key to Species of *Souzalopesmyia*

1 Vti divergent. Crossvein dm-cu oblique, weakly curved (Albuquerque 1951: Fig. 13); female: 2 frontals . . . . . *S. carioca* Albuquerque

– Vti parallel. Crossvein dm-cu oblique, almost straight (Albuquerque 1951: Fig. 11); female: 3 frontals 2

2 (1) Dc 2: 3; male: postocular row of setulae incomplete, not reaching epistome; setulae black; female: some acr prst stronger than the ground setulae . . . . . *S. amazonica* Albuquerque

– Dc 1: 3; male: postocular row of setulae complete; setulae black and yellow, the latter beginning after basal half of eye; female: acr prst undifferentiated from the ground setulae 3

3 1 proepisternal seta weak, about ¾ length of the upper anepisternal setae; male: fifth sternite without sharp depression on posterior side (Fig. 1); cercal plate heart-shaped (Fig. 4) . . . . . *S. paraensis* Carvalho, new species

– 1 proepisternal seta strong, similar to the upper anepisternal setae; male: fifth sternite with sharp depression on posterior side (Figs. 2, 3); cercal plate rounded (Figs. 5, 6) 4

4 (3) Species ranging from 8.0 to 9.0 mm in length; posterior ktps strong, about 2 times the length of the anterior one; male: frontal setae both cruciate; fifth sternite as in Fig. 2; cercal plate as in Fig. 5 . . . . . *S. singularis* (Stein)

– Species ranging from 6.5 to 8.0 mm in length; posterior ktps very strong, about 3

times the length of the anterior one; male: lower frontal setae cruciate, upper reclinate; fifth sternite as in Fig. 3; cercal plate as in Fig. 6 . . . . . *S. sulina* Carvalho, new species

Souzalopesmyia amazonica
Albuquerque 1951

Souzalopesmyia amazonica Albuquerque 1951:56; Pont 1972:23 (Neotropical catalog); Carvalho et al. 1993: 84 (Neotropical catalog).

Diagnosis.—This species is very similar to *S. singularis* but, it can be easily distinguished from the other *Souzalopesmyia* species by dc 2:3 setae.

Description.—Male: *Head:* Frons broad, at narrowest point 0.21 of head width. Eye with only normal pubescence. Fronto-orbital plate, parafacial, face and gena silvery white. Fronto-orbital plate broad, broadening gradually from vertex to lunula; at vertex plate almost equal to diameter of anterior ocellus, at lunula equal to three times anterior ocellus. Frontal vitta broad, parallel to vertex. 2 pairs of strong frontal setae on lower ⅔ of frons, former cruciate and latter reclinate; 1 strong orbital, reclinate and divergent. Ocellar triangle black, reaching to insertion of orbital setae, with some setulae behind posterior ocellar setae. Vti strong and parallel. Postocular row incomplete, reaching as single row just below mid level of eye and composed of black setulae. Gena below lowest eye margin equal to twice diameter of the anterior ocellus. Palpi slender, yellow.

Thorax: Ground color yellow, scutum dusted with whitish-grey. Dc 2:3; 5–6 rows of prst acr setulae; 11–12 rows of post acr setulae. 1 proepisternal weak, about ¾ length of upper anepisternal setae. Posterior ktps strong, about 2.5 times length of anterior one. Scutellum with 1 strong pair of apical and 1 subbasal setae; 1 preapical weak but stronger than ground setulae; disc with setulae descending below strong setae; bare ventrally.

Legs: Yellow. Fore femur with complete rows of AV and D setae; AD row weak and just to apical ⅔. Mid tibia with 3 P setae. Hind tibia with 5 AV setae on apical half (Albuquerque 1951: 57).

Wings: Clear, veins yellow. Membrane entirely covered with microtrichia. Crossvein r-m placed before point where vein R1 enters costa. Crossvein dm-cu oblique, almost straight. Calypters and haltere yellow.

Abdomen: Ground-color yellow; in posterior view; with a narrow black stripe on tergite 1 which is enlarged on tergite 3, 4 and 5 (Albuquerque 1951: Fig. 16). Tergite 4 and 5 with 2 strong apical setae.

Terminalia: See Albuquerque 1951: Fig. 12.

Measurements: Length of body, 7 mm (n = 1). Length of wings, 6 mm (n = 1).

Female: Differs from male as follows: *Head:* Frons at narrowest point 0.27 of head width. Frontal vitta broad, divergent to vertex. 3 pairs of strong frontals, former 2 cruciate. Ocellar triangle black, not reaching to insertion of 3rd pair of frontals. Some acr prst stronger than ground setulae. Crossvein dm-cu oblique, more than in male.

Terminalia: See Albuquerque 1951: Fig. 17, 18.

Measurements: Length of body, 8 mm (n=1). Length of wings, 8 mm (n = 1).

Remarks.—Adults have been collected in the afternoon on flowers and at night.

Type material examined.—Holotype ♂ in MNRJ labelled as follow: "35/Manaus—no centro [in the center of the city]/ à noite [at night]/15.vi.933 [15 June 1933]/Ant. [Antonio] Paes Filho" [hand label]; Souzalopesmyia/amazonica sp.n./30.8.50 [30 August 1950 [examined Albuquerque' date] / D. Albuquerque det." [Albuquerque hand label]; "Holotipo [holotype]" [red label]. Specimen in good condition (Lopes et al. 1997). Right fore tarsi, median and hind legs missing. Segments of the abdomen mounted on slide in Canada balsam.

Other examined material.—Total: 1. BRAZIL. Amazonas: Manaus, Ant. Paes Filho, 26.V.1933 (1 ♀ allotype MNRJ).

Souzalopesmyia carioca
Albuquerque 1951

Souzalopesmyia carioca Albuquerque 1951:53; Pont 1972: 23 (Neotropical catalog); Carvalho et al. 1993: 85 (Neotropical catalog).

Diagnosis.—*S. carioca* is one of the largest *Souzalopesmyia* species and can be distinguished from the other species by the divergent vti. The female has only 2 frontal setae.

Description.—Male: *Head:* Frons broad, at narrowest point 0.24 of head width. Eye with only normal pubescence. Fronto-orbital plate, parafacial, face and gena silvery white. Fronto-orbital plate broad, broadening gradually from vertex to lunula, at vertex plate almost equal to diameter of anterior ocellus, at lunula 3 times diameter of anterior ocellus. Frontal vitta broad, parallel to vertex. 2 pairs of strong cruciate frontals on lower ⅔ of frons; 1 strong orbital reclinate and divergent. Ocellar triangle reaching to insertion of orbital setae. Vti strong, divergent. Postoculars in a complete single row, reaching to epistome and composed of black setulae. Gena below lowest eye margin equal to twice diameter of anterior ocellus. Palpi slender, yellow.

Thorax: Ground-color yellow with scutum dusted with whitish grey. Dc 1:3; 6–7 rows of prst acr setulae; 11–12 rows of post acr setulae. 1 proepisternal seta very weak, about half length of upper anepisternal setae. Posterior ktps strong, about twice length of anterior one. Scutellum with 1 strong pair of apical and 1 subbasal setae; 1 preapical weak but stronger than ground setulae; disc with setulae descending below strong setae; bare ventrally.

Legs: Yellow. Fore femur with a complete row of AV, D and AD setae, latter weakest. Mid femur with 2–3 PV setae in basal half, shorter than femoral depth. Mid tibia with 2–3 P setae. Hind femur with 1 strong preapical AV seta, longer than femoral depth; AD row complete; 1 PD, 1 D, 1 AD preapical setae weaker than AV seta. Hind tibia with 4 AV setae on apical half.

Wings: Clear, veins yellow. Membrane entirely covered with microtrichia. Crossvein r-m placed before point where vein R1 enters costa. Crossvein dm-cu oblique, weakly curved in median part. Calypters and haltere yellow.

Abdomen: Ground-color yellow; tergite 3 and 4 each with blackish markings increasing in size to posterior margin in posterior view; tergite 5 blackish, except hind margin (Albuquerque 1951: Fig. 3). A median black stripe on tergites 3, 4 and 5. Tergite 4 and 5 with 2 strong apical setae.

Terminalia: See Albuquerque 1951: Fig. 4–10.

Measurements: Length of body, 8 mm (n = 1). Length of wings, 8 mm (n = 1).

Female: Differs from male as follows:

Head: Frons at narrowest point 0.27 times maximum head width. Frontal vitta broad, divergent to vertex. 2 pairs of strong frontals, cruciate. Ocellar triangle black, not reaching insertion of 2nd pair of frontals.

Terminalia: See Albuquerque 1951: Fig. 14, 15.

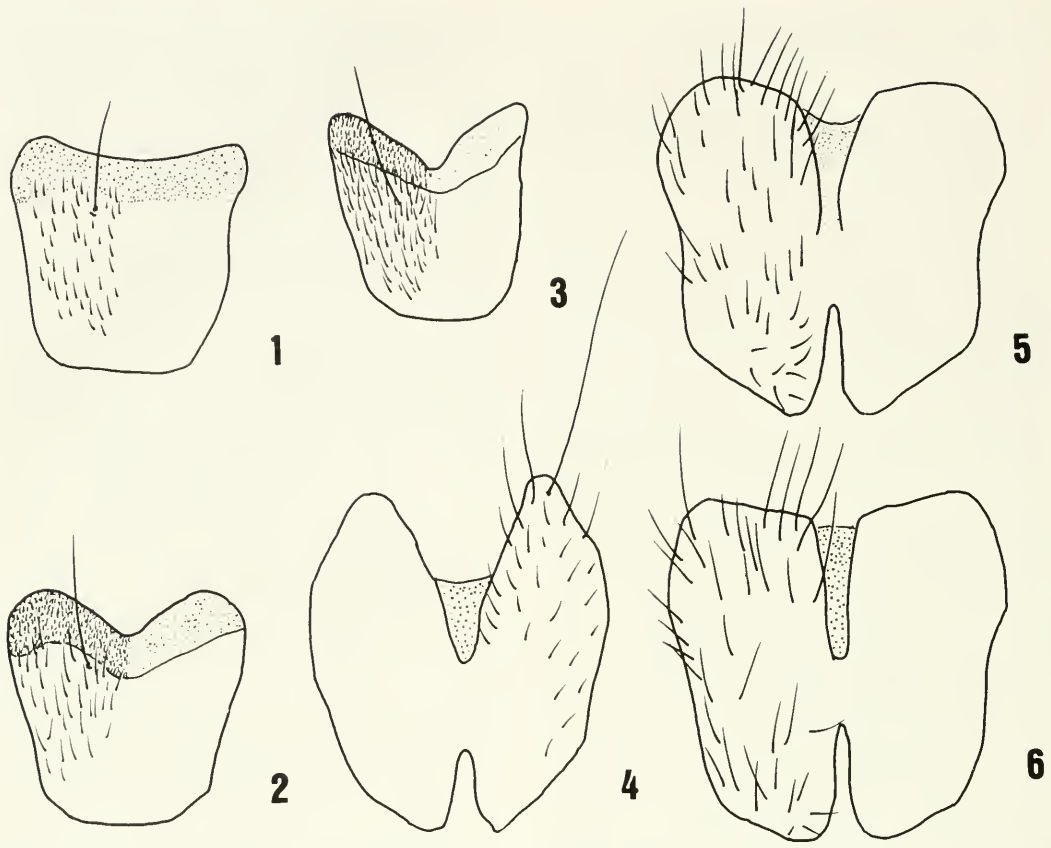
Measurements: Length of body, 8.5 mm (n=1). Length of wings, 8.5 (n = 1).

Type material examined.—Holotype ♂ in MNRJ labelled as follow: "Grajahu/Rio de Janeiro/Lopes [Hugo de Souza Lopes]-6.I.40 [6 January 1940]"; Souzalopesmyia/carioca sp.n./30.8.50 [30 August 1950] [examined Albuquerque date] /D. Albuquerque det." [Albuquerque hand label]; "Holotipo [holotype]" [red label]. Specimen in good condition (Lopes et al. 1997). Right wing on a slide mounted attached of pin holotype. Segments of abdomen on a slide mounted.

Other examined material.—Total: 1. BRAZIL. Rio de Janeiro: Rio de Janeiro, H.S. Lopes, 6.VI.1940 (1 ♀ allotype MNRJ).

Souzalopesmyia paraensis
Carvalho, new species
(Figs. 1, 4, 7, 10, 13, 14, 15)

Diagnosis.—*Souzalopesmyia paraensis* can be distinguished from the other *Souz-*



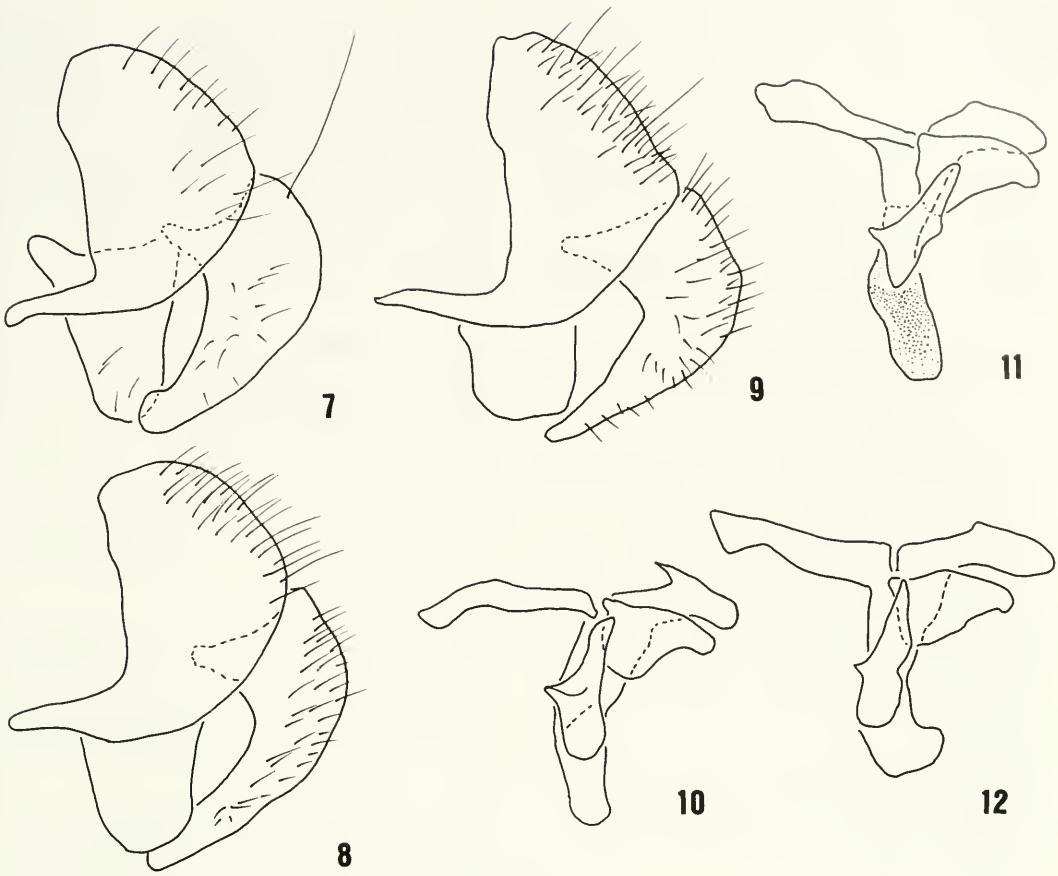
Figs. 1–6. 1–3, Male fifth sternite, dorsal view. 1, *Souzalopesmyia paraensis*. 2, *S. singularis*. 3, *S. sulina*. 4–6, Cercal plate, dorsal view. 4, *S. paraensis*. 5, *S. singularis*. 6, *S. sulina*.

alopesmyia species by male cercal plate rounded in outline and fifth sternite without posterior depression.

Description.—Male: *Head:* Frons broad, at narrowest point 0.21 of head width. Eye with only normal pubescence. Fronto-orbital plate, parafacial, face and gena silvery white. Fronto-orbital plate broad, broadening gradually from vertex to lunula, at vertex plate less than diameter of anterior ocellus, at lunula 3 times diameter of anterior ocellus. Frontal vitta broad, parallel to vertex. 2 pairs of strong cruciate frontal setae on lower ⅔ of frons; 1 strong orbital reclinate. Ocellar triangle reaching insertion of orbital setae. Vti strong, parallel. Postoculars in a complete single row, reaching epistome and composed of black and yellow setulae; latter beginning after basal half of eye and reaching epistome, but 1–2 with black setulae. Gena below lowest eye margin twice diameter of anterior ocellus. Palpi slender, yellow.

Thorax: Ground-color yellow, dusted with whitish grey. Dc 1:3; 7–8 rows of prst acr setulae; 10–11 rows of post acr setulae. 1 proepisternal seta weak, about ¾ length of the upper anepisternal setae. Posterior ktps strong, twice length of anterior one. Scutellum with 1 strong pair of apical and 1 subbasal setae, 1 preapical weak but stronger than ground setulae; disc with setulae descending below strong setae; bare ventrally.

Legs: Yellow. Fore femur with a complete row of AV and D setae; AD row weak. Mid femur with 2 PV setae in basal half, not equal to femoral depth. Mid tibia



Figs. 7–12. 7–9, Epandrium, cercal plate and surstylus, lateral view. 7, *Souzalopesmyia paraensis*. 8, *S. singularis*. 9, *S. sulina*. 10–12, Phallus and associated structures, lateral view. 10, *S. paraensis*. 11, *S. singularis*. 12, *S. sulina*.

with 3 P setae. Hind femur with 1 strong preapical AV seta, longer than femoral depth; AD row complete; 1 PD, 1 D, 1 AD preapical seta weaker than AV seta. Hind tibia with 4 AV setae on apical half.

Wings: Clear, veins brownish. Membrane entirely covered with microtrichia. Crossvein r-m placed before point where vein R1 enters costa. Crossvein dm-cu oblique, almost straight. Calypters and haltere yellow.

Abdomen: Ground-color yellow; in posterior view with a narrow, slight, black stripe on tergite 1 which is blackish and enlarged on tergites 3, 4 and 5. Tergite 4 and 5 with 2 strong apical setae.

Terminalia: See Figs. 1, 4, 7, 10, 13.

Measurements: Length of body, 8.5 mm (n = 1). Length of wings, 6.6 (n = 1).

Female: Differs from male as follows: *Head:* Frons at narrowest point 0.31 of head width. Frontal vitta broad, divergent to vertex. 3 pairs of strong frontals, first one cruciate, second one reclinate and convergent and third one reclinate and divergent. Ocellar triangle black, not reaching insertion of 3rd pair of frontals. Postoculars in a complete single row, with black setulae.

Measurements: Length of body, 8.5–9.0 mm (n = 2). Length of wings, 7.0–7.7 mm (n = 2).

Type material examined.—Holotype ♂ in MPEG, labelled as follow: "Belém Mo-

cambo/ 01-IV-1977"; "Brasil Pará/A.Y. Harada."

Other examined material.—Total: 2 paratypes: BRASIL. Pará: Belém. A. Y. Harada, 1.IV.1977 (1 ♀ DZUP); ibidem, same collector, 6.IV.1977 (1 ♀ MPEG). Specimen in reasonable condition. Left fore and right mid legs missing; left mid tarsi and hind right leg glued on to a card attached to the pin.

Souzalopesmyia singularis (Stein 1911)
(Figs. 2, 5, 8, 11, 16)

Mydaea singularis Stein 1911:91; Stein 1919: 124 (world catalog); Séguy 1937: 282 (world catalog).

Peruvia singularis; Malloch 1929: 105 (type species of *Peruvia*); Hennig 1965: Fig. 31 (tip of female ovipositor).

Souzalopesmyia singularis; Pont 1972: 24 (Neotropical catalog); Carvalho et al. 1993: 85 (Neotropical catalog).

Diagnosis.—*Souzalopesmyia singularis* can be distinguished from the other *Souzalopesmyia* species by posterior depression on male fifth sternite and 2 cruciate frontal setae.

Description.—Male: *Head:* Frons broad, at narrowest point 0.23 of head width. Eye with only normal pubescence. Fronto-orbital plate, parafacial, face and gena silvery white. Fronto-orbital plate broad, broadening gradually from vertex to lunula, at vertex plate less than diameter of anterior ocellus, at lunula 2.5 times diameter of anterior ocellus. Frontal vitta broad, parallel to vertex. 2 pairs of strong cruciate frontals on lower ⅔ of frons; 1 strong orbital reclinate. Ocellar triangle reaching insertion of orbital setae. Vti strong parallel. Postoculars in a complete single row, reaching epistome and composed of black and yellow setulae; latter beginning after basal half of eye and reaching epistome, but 1–2 with black setulae. Gena below lowest eve margin equal to 2.5 times diameter of the anterior ocellus. Palpi slender, yellow.

Thorax: Ground-color yellow with scutum dusted with whitish-grey. Dc 1:3; 5–6 rows of prst acr setulae; 9–10 rows of post acr setulae. 1 proepisternal seta similar to upper anepisternal setae. Posterior ktps strong, twice length of anterior ones. Scutellum with 1 strong pair of apical and 1 subbasal setae; 1 preapical weak, but stronger than ground setulae; disc with setulae descending below strong setae; bare ventrally.

Legs: Yellow. Fore femur with complete row of AV and D setae; AD row weak. Mid femur with 2 PV setae in basal half, less than femoral depth. Mid tibia with 3 P setae. Hind femur with 1 strong preapical AV seta, longer than femoral depth; AD row complete; 1 PD, 1 D, 1 AD preapical setae weaker than AV seta. Hind tibia with 5 AV setae on apical half.

Wings: Clear, veins brownish. Membrane entirely covered with microtrichia. Crossvein r-m placed just before point where vein R1 enters costa. Crossvein dm-cu oblique, almost straight. Calypters and haltere yellow.

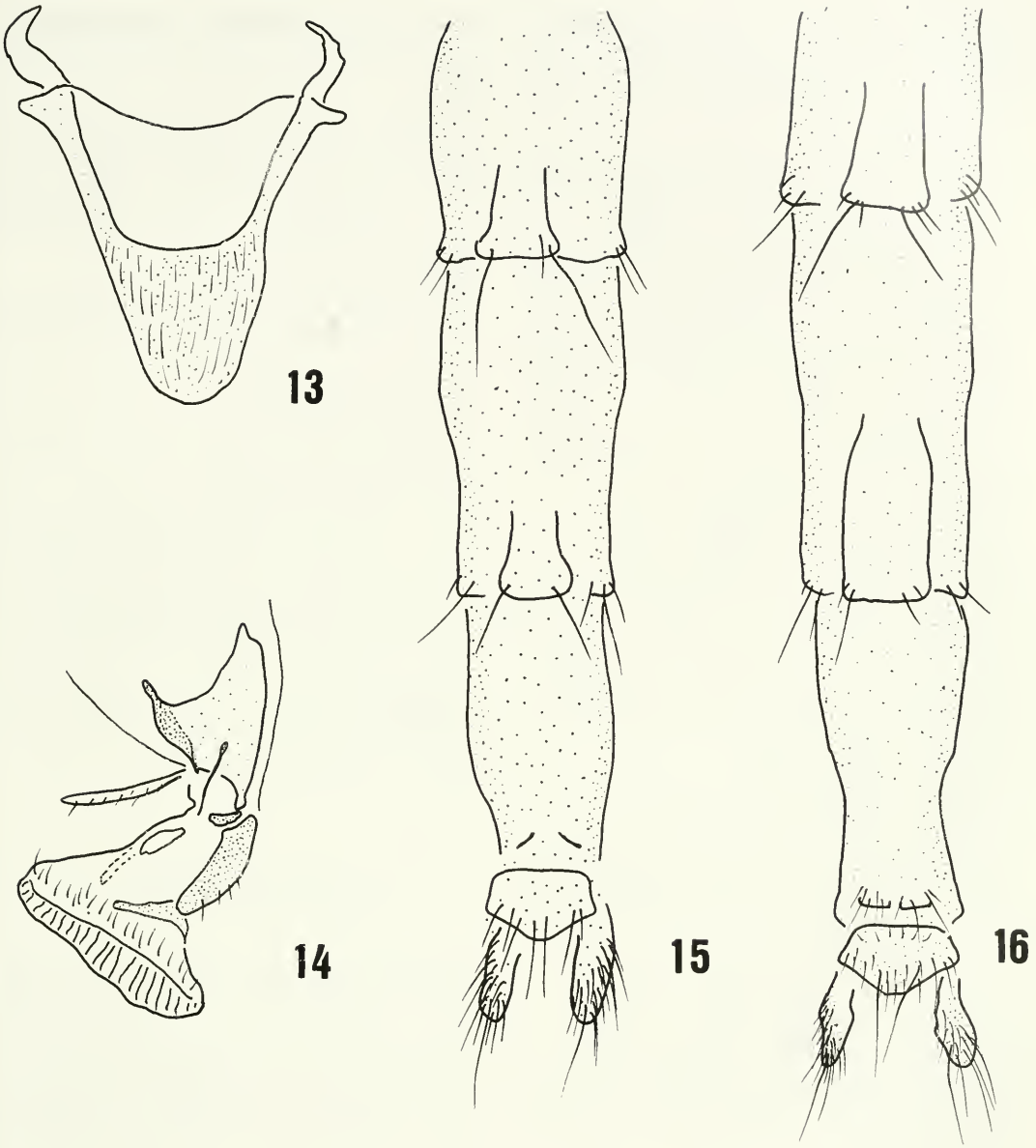
Abdomen: Ground-color yellow; in posterior view with slight narrow black stripe on tergite 1 which is enlarged on tergite 3, 4 and 5. Tergite 4 and 5 with 2 strong apical setae.

Terminalia: See Figs. 2, 5, 8, 11.

Measurements: Length of body, 8 mm (n = 1). Length of wings, 7.5 mm (n = 1).

Female: Differs from the male as follows: *Head:* Frons at narrowest point 0.32 times maximum head width. Frontal vitta broad, divergent to vertex. 3 pairs of strong frontals, first one cruciate, second one reclinate and convergent and third one reclinate and divergent. Ocellar triangle not reaching insertion of 3rd pair of frontals. Postoculars in a complete single row of black setulae.

Measurements: Length of body, 8.5–9.0 (n = 3). Length of wings, 8.0–8. 5 mm (n = 3). Type material examined. Holotype male in SMT labelled as follow: "Bolivia-Mapiri/ 14.III.03 [hand written]/Sarampioni 700 m [green label]": "Coll W. Schnuse/



Figs. 13–16. 13–15, *Souzalopesmyia paraensis.* 13, Hypandrium, dorsal view. 14, Proboscis, lateral view. 15, Ovipositor, ventral view. 16, Ovipositor of *S. singularis,* ventral view.

1911-3"; "Mydaea/singularis/ sp.n. [light green hand written label]: "Typus" [red label]; "Staatl. Museum fur/ Tierlunde Dresden." Specimen in good condition lacking the left hind leg and hind right tarsi. Abdomen in microvial with glycerine.

Other examined material.—Total: 3. BOLIV1A: Mapiri, Sarapioni, 700–800 m, W. Schnuse, III-1903 (2 ♀ SMT); S. Carlos, W. Schnuse, I-1901 (1 ♀ SMT).

Souzalopesmyia sulina Carvalho, new species

(Figs. 3, 6, 9, 12)

Diagnosis.—*Souzalopesmyia sulina* is one of the smallest *Souzalopesmyia* species.

It can be distinguished from the other *Souzalopesmyia* species by deeply posterior depression on male fifth sternite and 2 frontal setae, latter reclinate.

Description.—Male: *Head:* Frons broad. at narrowest point 0.25 of head width. Eye with only normal pubescence. Fronto-orbital plate, parafacial, face and gena silvery white. Fronto-orbital plate broad, broadening gradually from vertex to lunula, at vertex plate about equal to diameter of anterior ocellus, at lunula 2.5 times diameter of anterior ocellus. Frontal vitta broad, parallel to vertex. 2 pairs of strong frontal setae on lower ⅔ of frons; former cruciate and latter reclinate; 1 strong orbital reclinate and divergent. Ocellar triangle black, reaching insertion of orbital setae. Vti strong and parallel. Postoculars in a complete single row, reaching epistome and composed of black and yellow setulae; latter beginning after basal half of eye and reaching epistome, but 1–2 with black setulae. Gena below lowest eye margin twice diameter of anterior ocellus. Palpi slender, yellow.

Thorax: Ground-color yellow with scutum dusted with whitish-grey, more evident in pre sutural area. Dc: 1:3; 5–6 rows of prst acr setulae: 11–12 rows of post acr setulae. 1 proepisternal seta strong, similar to upper anepisternal setae. Posterior ktps very strong, about 3 times length of anterior one. Scutellum with 1 strong pair of apical and 1 subbasal setae; 1 preapical weak but stronger than ground setulae; disc with setulae descending below strong setae; bare ventrally.

Legs: Yellow. Fore femur with complete rows of AV and D setae; AD row weak. Mid femur with 2–3 PV setae in basal half, less than femoral depth. Mid tibia with 3–4 P setae. Hind femur with 1 strong preapical AV seta, longer than femoral depth; AD row weak and complete; 1 PD, 1 D, 1 AD preapical seta weaker than AV seta. Hind tibia with 4–5 AV setae on apical half.

Wings: Clear, veins brownish. Membrane entirely covered with microtrichia, crossvein r-m placed just before point where vein R1 enters costa. Crossvein dm-cu oblique, almost straight. Calypters and haltere yellow.

Abdomen: Ground-color yellow; in posterior view with a narrow black stripe on tergite 1 which is enlarged on tergite 3, 4 and 5. Tergite 4 and 5 with 2 strong apical setae.

Terminalia: See Figs. 3, 6, 9, 12.

Measurements: Length of body, 6.5–8.0 mm (n = 5). Length of wings, 6.5–7.7 mm (n = 5).

Female: Unknown.

Remarks.—Adults have been collected with Malaise traps.

Type material examined.—Holotype ♂ in MHPA labelled as follow; "Depto Canindeyu/Reserva Natural del Bosque/Mbaracayu: Jejui-mi/Malaise 3, bosque bajo inundado/ Colr. A.C.F. Costa/ 10-18.VIV1996 [18 July 1996]"; "Holotipo [holotype]" [red label].

Other material examined.—Total: four paratypes. Same label of the holotype: 2 ♂, 10–18 July 1996 [DZUP, MHPA], 2 ♂, 18–28 July 1996 [DZUP, MHPA].

Discussion

Phylogenetic Analysis

Phylogenetic studies on Muscidae are still scarce (Carvalho 1989d). The family contains about 200 genera with well over 4,000 species worldwide (Pont 1989, Carvalho et al. 1993). The family is undoubtedly monophyletic (Hennig 1965, McAlpine 1989, Michelsen 1991), but historically the Muscidae has included groups that are doubtfully monophyletic (Carvalho 1989d).

Several genera of Phaoniinae in the Neotropics (Pont 1972), a paraphyletic subfamily pointed by Hennig (1965) and recently by Carvalho (1989b), were transferred to other subfamilies (Carvalho 1985, 1989a, 1989b, 1989c, Couri and Lopes 1986, Carvalho & Pont 1998). Currently the subfamily in the region has only four genera (Carvalho et al. 1993): *Dolichophaonia* Carva-

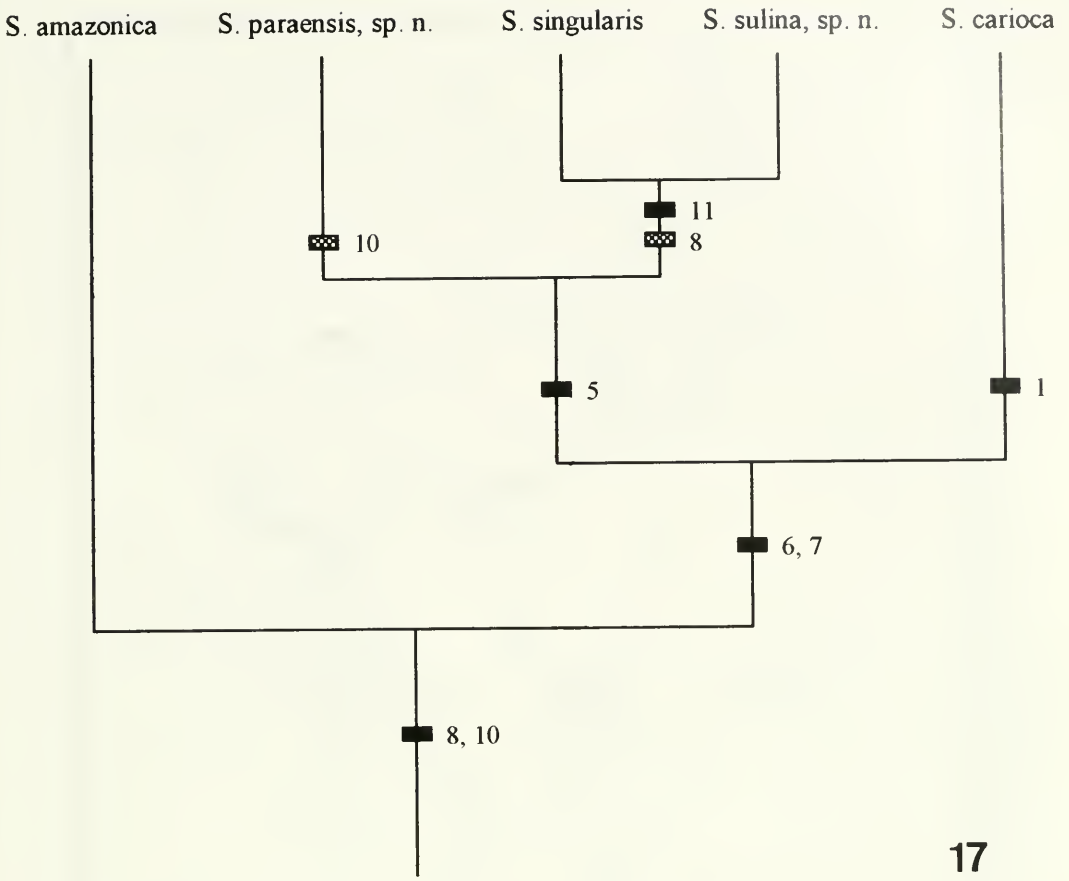


Fig. 17. Cladogram of species of *Souzalopesmyia*. Synapomorphies = solid black rectangles; reversal = dotted rectangles. Character numbers correspond to those stated in Table 1.

lho, 1993; *Helina, Phaonia* and *Souzalopesmyia*.

Souzalopesmyia is a small and isolated clade, apparently representing an ancient lineage of Phaoniinae. The species of genus have head elongate which is commonly correlated with broad male frons (Vockeroth 1972). But these lengthening is considered independent from that in the some genera in the subfamilies Atherigoninae, Cyrtoneurininae, Azeliinae-Reinwardtiini or Mydaeinae.

The Hennig86 phylogenetic analysis of *Souzalopesmyia* was based on seven characters (with an asterisk in Table 1) and resulted in a single tree shown in Fig. 17 (length = 9 steps, consistency index = 0.77, retention index = 0.75).

Biogeography

Hennig (1965) argued that the first invasion (Edentata level) of the Neotropical Muscidae fauna may have come from the Northern Hemisphere during the Upper Cretaceous or Early Tertiary period. This time frame was also suggested by Michelsen (1991) for the invasion of the basal clade of the Anthomyiidae, *Coenosopsia* + *Phaonantho*, into South America.

There are few papers on biogeography of Muscidae, none of them of Neotropical Region, except Hennig (1965). In Holarctic Region, all taxa of the *Eudasyphora* s. str. Townsend (Muscinae) are faunal elements of known dispersal centers (Cuny 1980). The speciation of these flies, were correlat-

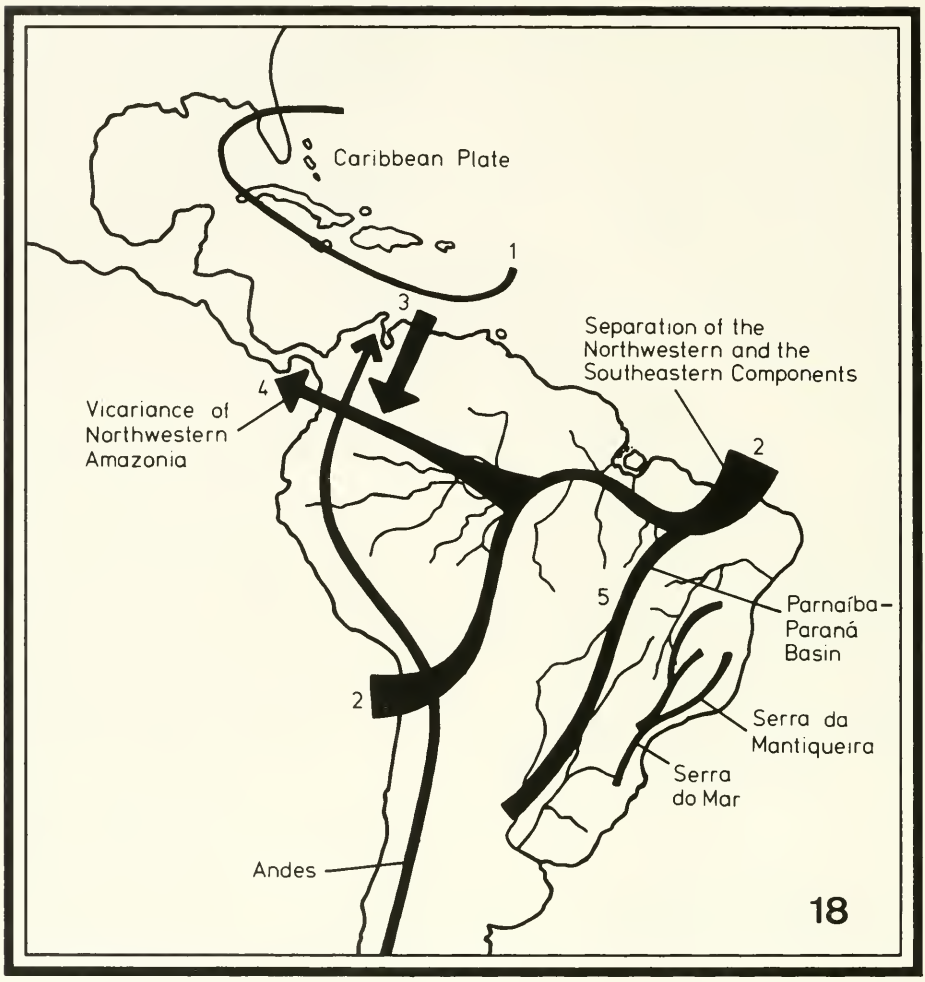


Fig. 18. A summary of the main vicariance barriers in the history of the Neotropical region. I = Carribbean Plate detachment from the mainland. 2 = Separation between the Northwestern and the Southeastern main components, a line along the Rivers Amazonas/Madeira/Mamoré in the Amazonian Basin. 3 = Epicontinental sea formation in the Maracaibo area. 4 = A large division in northwestern Amazonia (not related to date to any geological event). 5 = Middle to Late Cretaceous water connection between the Parnaíba Basin and the Paraná Basin (redrawn from Amorim and Pires 1996).

ed with the history of the forest vegetation during the Pleistocene (Cuny 1980).

Amorim and Pires (1996), corroborated independently by Grazia (1997), indicated that the first division in the continental region of the Neotropics was in the Late Cretaceous, showing a northwestern track against a southeastern track (Fig. 18). Alike pattern is showed by Camargo (1996) for some bees (Meliponini, Apinae, Apidae) in Neotropical Region. However, this latter biogeographical reconstruction was postulated by modification occurred by the changing forests in the Pleistocene.

Souzalopesmyia, based on the position of *S. amazonica* as the basal clade of genus, may have had its ancestor back in the Late Cretaceous (Fig. 19). This age for the genus is not unrealistic although no fossil record is known for family older than the Eocene (Evenhuis 1994). Pont and Carvalho (1997) studied three fossil species of Muscidae

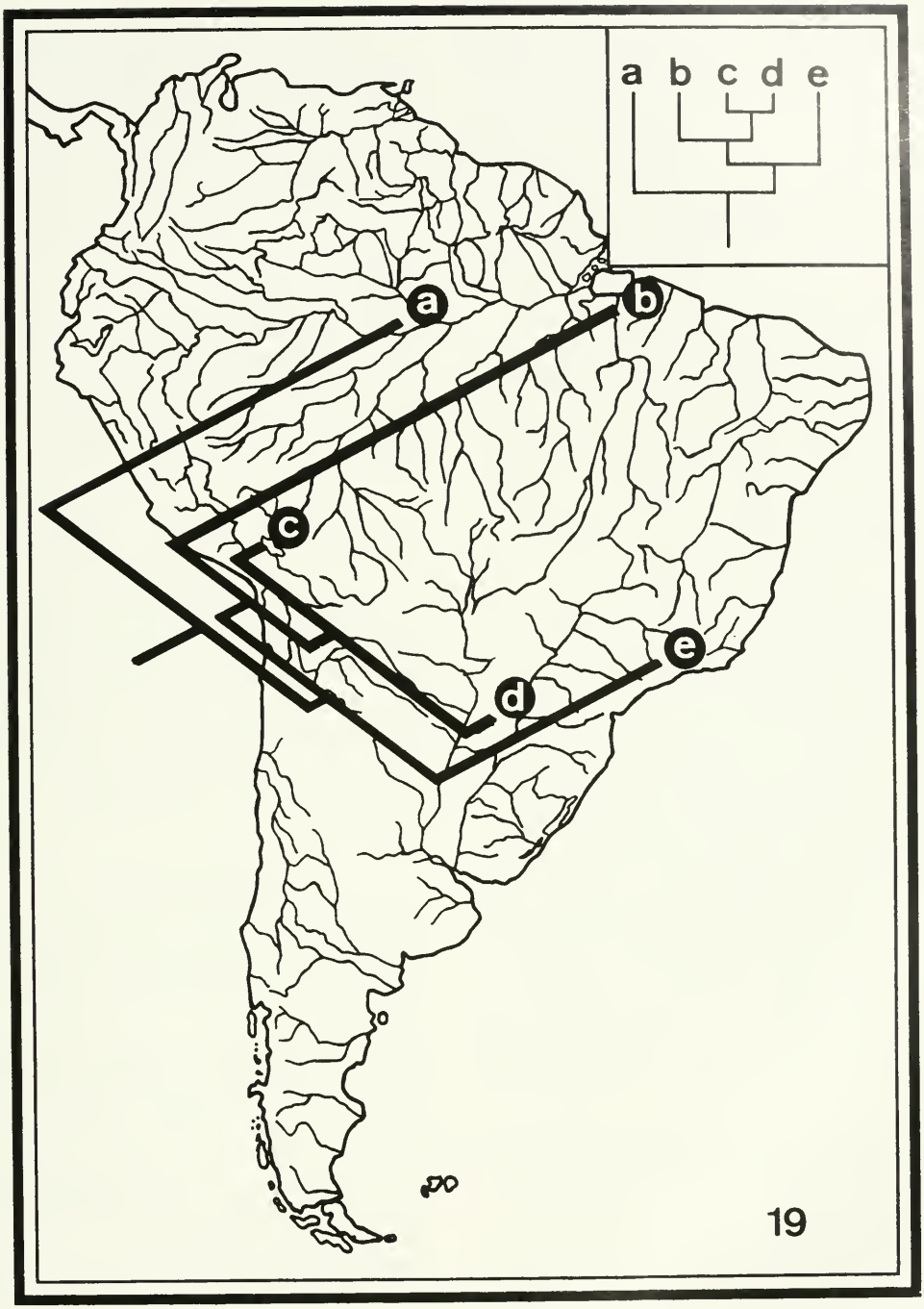


Fig. 19. Geographical distribution of species of *Souzalopesmyia*, with cladogram superimposed. a, *S. amazonica*. b, *S. paraensis*. c, *S. singularis*. d. *S. sulina*. e, *S. carioca*.

from Dominican amber dated from Miocene, 15–20 mya ago, two of which are *Phaonia* species. A cladogram by S. M. P. Coelho (unpublished Ph.D. thesis) suggests that the *Phaonia* fossil species have a more recent origin than the ancestor of *Souzalopesmyia*. The origin of the genus is therefore probably older than 15–20 mya, suggesting that *Souzalopesmyia* is one of the most basal genera of Phaoniinae in the Neotropics.

The origin of the Neotropical Phaoniinae fauna cannot be completely understood on the basis of the present paper. The ancestor of *Souzalopesmyia* may have reached South America by dispersal from North America (Hennig 1965), Africa or have evolved in the Neotropics. The discovery of the sister group of the genus is required.

The five species of *Souzalopesmyia* are morphologically similar and exhibit allopatric distribution suggesting that the terminal branches of this clade could be resulted from relatively recent speciation.

Nevertheless, the allopatric pattern of speciation of the genus cannot be fully explained with the available geological and biogeographical information. Most of the species are known from only a few specimens, suggesting that intensive effort may be necessary before reliable statements can be made about the distribution patterns of the species. Species of *Souzalopesmyia* are not expect to occur in western side of Andes as it requires tropical rainforest (Figs. 18, 19).

The occurrence of *S. paraensis* in Belém, along south side of the Amazon River, part of the northwestern track, could be the result of a single dispersal event (Figs. 18, 19) to colonize that region, in a more recent time, which belongs to the northwestern track.

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ASHLOCKOBIUS, A NEW GENUS OF MYODOCHINI FROM VENEZUELA (HEMIPTERA: LYGAEOIDEA: RHYPAROCHROMIDAE: MYODOCHINI)

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Abstract.—***Ashlockobius cursorius*, new genus and species** of myodochine lygaeoid is described from Venezuela. The genus is related cladistically to *Orthaea* Dallas, *Catenes* Distant, *Heraeus* Stål and *Myodocha* Latreille. It is believed to be an ant mimic. Figures are given of the details of the inflated phallus and of the claspers. A color figure of the habitus is included.

Key Words: Hemiptera, Lygaeoidea, Rhyparochromidae, Myodochini. Venezuela, *Ashlockobius cursorius*, mimicry

The Myodochini constitute one of the dominant elements in the lygaeoid fauna of the Neotropics. It is abundant and diverse not only in the number and variety of taxa present but in the abundance of many individuals of some species. Ant mimicry occurs frequently. The new genus described below is apparently an ant mimic although its biology is unknown.

Henry (1997) has elevated the former subfamily Rhyparochrominae of the family Lygaeidae to family status with two subfamilies, the Plinthisinae and the Rhyparochrominae with the former tribes of the latter retained as tribes. We have adopted Henry's conclusions here, but suggest that the tribes within his new definition of the subfamily may ultimately prove to merit family status cladistically. Henry's statement that the subfamily Rhyparochrominae as redefined consists of taxa with an incomplete suture between abdominal sterna four and five and with carinate pronotal margins is an oversimplification. Genera that occur in at least five tribes within the Rhyparochrominae have the abdominal sternal suture complete. Rounded, ecarinate pronota occur in several tribes and is one of the diagnostic features of the Myodochini.

All measurements are in millimeters.

Ashlockobius Slater and Slater, new genus

Description.—Body elongate, slender, nearly parallel sided. Dorsal surface of body subshining. Legs and antennae both extremely elongate. Head moderately declivent anteriorly; eyes set a short distance away from anterior pronotal angles. Antenniferous tubercules divergent. Head below broadly transversely striate from level of distal ends of antenniferous tubercles to level of posterior margins of eyes. Bucculae V-shaped. Vertex convex between eyes with patches of pruinosity present.

Anterior pronotal lobe extremely elongate and elliptically convex, with a pruinose median stripe on anterior pronotal lobe and large irregular pruinose patches laterally on posterior half of anterior lobe. Posterior pronotal lobe dull with a patch of white pruinosity near transverse impression on either side of midline. Pronotum with only scattered, relatively inconspicuous, punc-

tures present; anterior collar complete, coarsely punctate, delimited posteriorly by a sharp deeply impressed line, not produced posteriorly at meson; transverse pronotal impression deep and complete; posterior pronotal lobe with prominent punctures.

Scutellum with a conspicuous Y-shaped, elevated carina; pruinose, bicolored with a large triangular basal grayish-white patch and a spot on each side near divergence of elevated Y-carina, remainder of scutellum reddish brown. Clavus, corium and membrane contrastingly strongly shining former with 3 complete rows of punctures and a partial fourth row on distal half between inner and median rows. Corium moderately expanded posteriorly; outer margin irregular and beaded, lacking a stridulitrum. Apical corial margin adjacent to membrane lacking a series of punctures. Mesepimeron not emergent. Metathoracic scent gland auricle short, straight, tapering distally; evaporative area large, covering inner two thirds to three fourths of metapleuron, and extending narrowly along posterior margin of mesopleuron.

Fore coxa with a prominent spine and a smaller secondary spine present. Fore femur elongate and slender, almost entire ventral surface of each femur heavily spinous, with rows of large spines along inner and outer edges and numerous small spines between. Each fore tibia with a widely spaced series of 4 short sharp spines on inner face. Shaft of tibia not strongly curved.

Lateral and ventral surfaces completely dull and chiefly pruinose except for a large quadrate shining patch mesally on mesosternum, this latter with a narrow median groove. Antenna very elongate, slender, terete with fourth segment fusiform. Posterior margin of abdominal sternum 2 not finely scalloped.

Posterior margin of pygophore broadly rounded, without a median impression. Clasper (Fig. 3) with a distinct thumb-like exterior projection, interior margin with a pronounced flange narrowing distally but extending almost to apex. Phallus (Figs. 2, 4) without sclerotized conjunctival or vesical spines; conjunctiva short, bearing low lateral subapical lobes; vesica short; helicoid process present; a large lobe bearing many projections on each side of ejaculatory reservoir. Ejaculatory reservoir with well developed wings (Fig. 2), holding sclerites short, narrowing distally.

Type species.—*Ashlockobius cursorius,* new species. Monotypic.

Discussion.—*Ashlockobius* keys without difficulty to couplet 51 in Harrington's (1980) key to myodochine genera. It differs from *Togo* Bergroth (from Japan) in having a relatively much longer anterior pronotal lobe, more than one and one-half times the length of the posterior lobe in *Ashlockobius*; in *Togo* the anterior lobe is at most only slightly longer than the posterior lobe. *Ashlockobius* also does not have strongly curved anterior tibiae. Most specimens of *Togo* are brachypterous, the male fore tibiae are prominently curved, and the members of the genus are relatively stout and robust.

Ashlockobius differs from those genera reached through couplet 52 of Harrington by having the combination of armed male fore tibiae, as described above, and an anterior pronotal lobe at least 1.5 times as long as the posterior lobe.

The absence of vesical or conjunctival spines and the robustly winged ejaculatory reservoir with short holding sclerites places *Ashlockobius* in the group of genera with Harrington's Type IV phallus. This placement is supported by the broadly rounded posterior margin of the pygophore (Fig. 5). Within this group the presence of pruinose areas on the dorsum and the somewhat elongate head and rounded vertex place the genus with a group on Harrington's cladogram consisting of *Orthaea* Dallas, *Catenes* Distant, *Heraeus* Stål, and *Myodocha* Latreille. Analysis of other phallic characters must await study of the inflated phallus of more species. The illustration of an inflated *Myodocha* phallus provided by Ashlock (1957), which exhibits an elongate conjunctiva with several lobes and an apparently

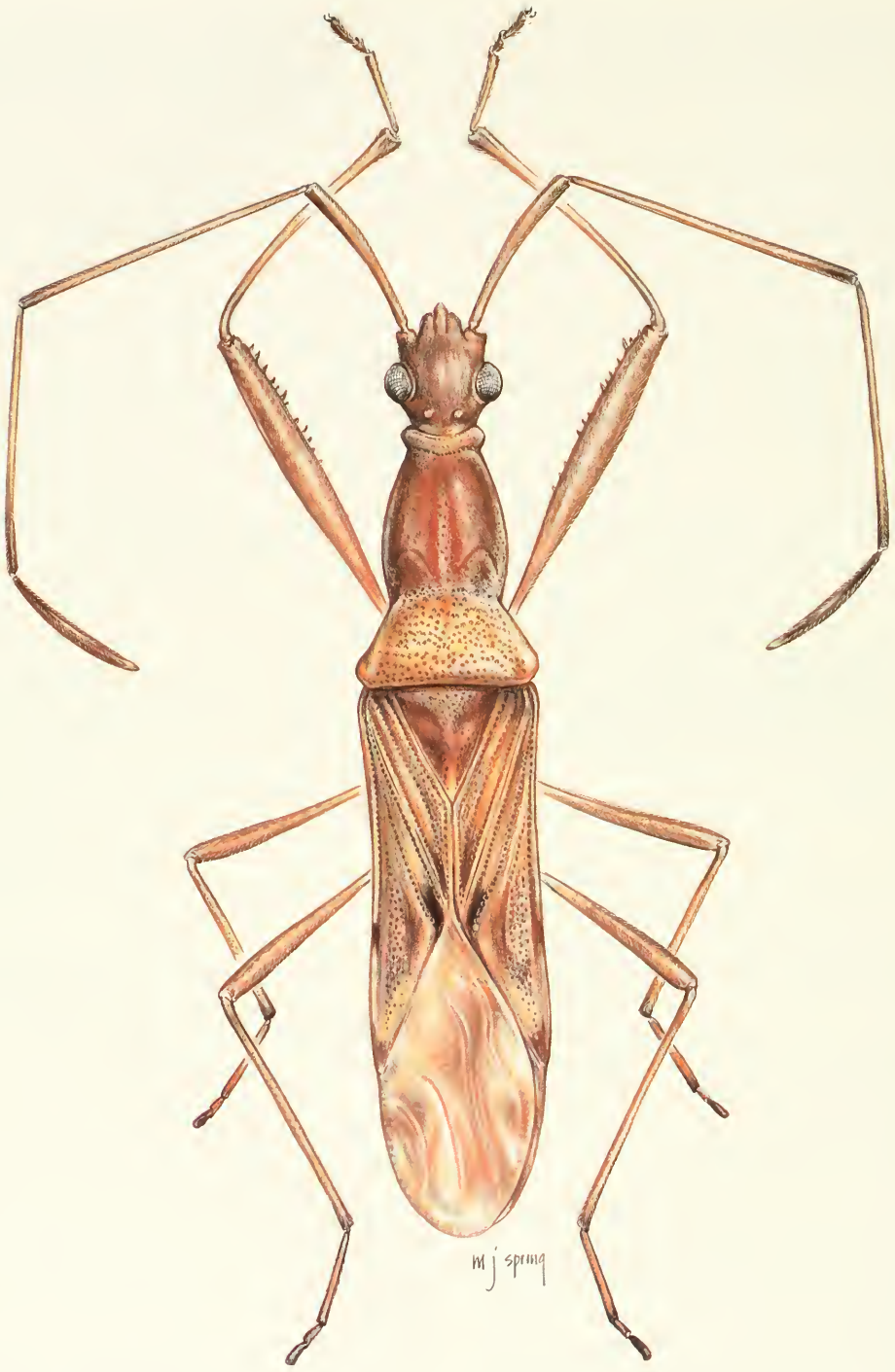
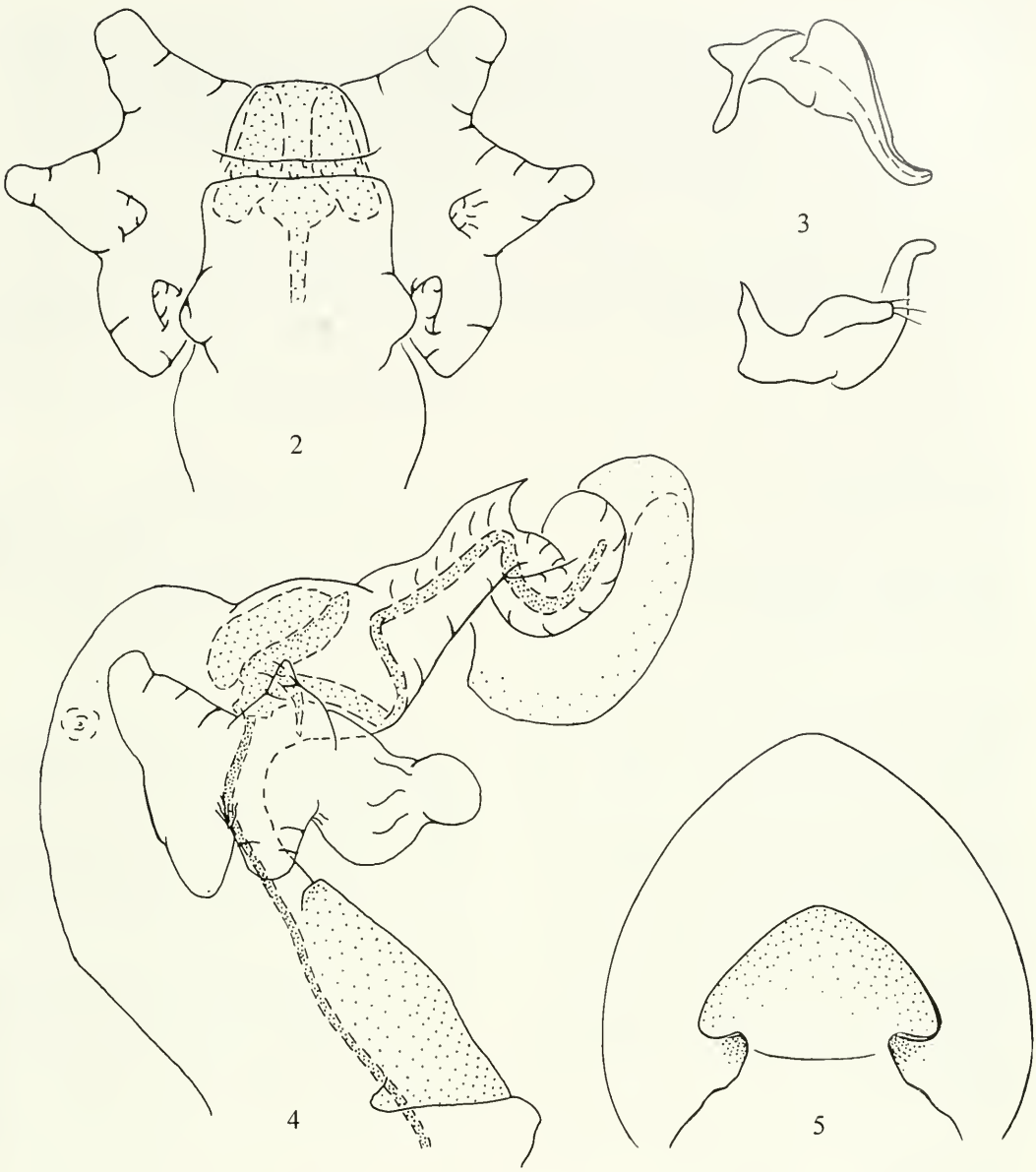


Fig. 1. *Ashlockobius cursorius*, Dorsal view.



Figs. 2–5. *Ashlockobius cursorius*. 2, Ejaculatory reservoir, dorsal view. 3, Claspers, outer and inner views. 4, Aedeagus, lateral view. 5, Genital capsule, dorsal view.

asymmetric set of vesical lobes, indicates that such studies will prove to be fruitful.

Etymology.—It gives us great pleasure to be able to dedicate this striking new genus to the memory of Dr. Peter D. Ashlock for his many contributions to the systematics of the Lygaeoidea.

Ashlockobius cursorius Slater and Slater, new species

(Figs. 1–5)

Description.—*Male:* Body very elongate, slender, attenuated, with extremely elongate appendages. Color bright reddish brown almost throughout, including ap-

pendages. Antenna with distal ends of segments II and III infuscated with chocolate brown. Corium marked with chocolate brown as follows: a small spot along lateral corial margin at level of distal third of apical corial margin, a small apical spot, an elongate dash along radial vein running from level of distal fifth of claval commissure nearly to anterior end of apical corial margin, a stripe at inner angle of corium that extends from inner margin at apical third of claval commissure to adjacent row of punctures then narrowly along apical corial margin to a level slightly posterior to lateral corial spot. Anterior collar and posterior pronotal lobe yellow, contrasting with red-brown anterior lobe. Corium light yellow brown except as noted above.

Eyes large, protrudant but not stalked, head strongly narrowing behind eyes but without a distinct stalked neck. Length head 1.34, width 1.20, interocular space 0.62. Length pronotum 2.60, length anterior pronotal lobe (less anterior collar) 1.60, width 1.84. Length scutellum 1.24, width 0.96. Length claval commissure 0.84. Midline distance apex clavus-apex corium 1.76. Midline distance apex corium-apex abdomen 1.72. Length labial segments I 0.76, II 0.84, III 0.52, IV 0.44. Labium reaching posterior third of prosternum but remote from fore coxae. Length antennal segments I 1.88, II 3.48, III 2.80, IV 1.72. Total body length 9.80.

Holotype.—♂. VENEZUELA: Aragua, 16 km S. Telerias, May 10, 1978 (C.W. & L.B. O'Brien and Marshall). In American Museum of Natural History, New York.

Etymology.—The name is from the Latin word for a runner.

Discussion.—The male specimen upon which the preceding description is based was collected in Venezuela twenty years ago. It is a striking, elongate, long-legged myodochine, which we have held for many years in the hope that additional specimens would become available. Unfortunately this has not happened.

Acknowledgments

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BIOSYSTEMATIC STUDIES OF CEYLONESE WASPS, XXII: *BETHSMYRMILLA*, A NEW GENUS OF MUTILLID WASPS (HYMENOPTERA: MUTILLIDAE: MYRMILLINAE)

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Abstract.—***Bethsmyrmilla alticola*, new genus and new species** is described from Sri Lanka. A key is given to the Oriental genera of Myrmillinae. The halictine bee *Lasioglossum (Sudila) alphenum* (Cameron) is the probable host of *B. alticola.*

Key Words: Mutillid wasps, *Bethsmyrmilla alticola,* new genus and new species, Sri Lanka, *Lasioglossum (Sudila) alphenum* (Cameron)

Borge Petersen estimated that the mutillid fauna of Sri Lanka was 74 species based on the literature (in litt. to KVK, 1976). He mentioned that he found 45–50 species among the specimens that he had borrowed. The latter figure, however, does not incorporate a study of all of the rich mutillid fauna collected during the later years, 1975–1981, of the Smithsonian's "Ceylon Insect Project" and two visits in 1993 and 1997 by K. V. Krombein and B. B. Norden. We anticipate that a study of these collections will result in a much more accurate inventory of the mutillid fauna.

During the latest trip to Sri Lanka, Beth Norden found two females of an unusual small mutillid wasp in the ground nests of the halictine bee *Lasioglossum (Sudila) alphenum* (Cameron). These wasps belong to a new genus and species that we place in the Myrmillinae because the side of the thorax is evenly concave, the mesopleuron has a strong supracoxal carina and the pronotal-mesopleural suture is lacking except a small section above. The subfamily presently comprises three genera in the Oriental region: *Spilomutilla* Ashmead, *Squamulotilla* sensu Mickel and *Bethsmyrmilla*, new genus.

The genus *Squamulotilla* Bischoff (type species *Squamulotilla denticollis* Bischoff, male, North Cameroon, Nigeria) includes seven Afrotropical species which are known from males only. For many years Guido Nonveiller has collected and studied the mutillid fauna of Cameroon. We support his opinion (1995) that true females of *Squamulotilla* are probably described in the Afrotropical genera *Clinotilla* Arnold (males still unknown). Oriental species placed in *Squamulotilla* by Mickel (1933, 1935) comprise several undescribed genera of Myrmillinae which will be treated separately.

Depositories for specimens listed are as follows:

IBPV	Institute of Biology and Pedology, Vladivostok, Russia.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. U.S.A.

Key to the Oriental Genera of Subfamily Myrmillinae

1. Female 2
– Male (unknown for *Bethsmyrmilla*) 4
2. Mandible widened apically, without subbasal tooth on inner margin (Fig. 8); gena dentate beneath; gastral tergum 2 posteriorly with three spots (Fig. 3) or a wide band of pale pubescence shallowly concave medially; gastral sternum 2 with median longitudinal carina ending usually in an acute tubercle ..... *Spilomutilla* Ashmead
– Mandible not widened apically, with subbasal tooth on inner margin (Figs. 6, 7, 9); gena not dentate beneath; gastral tergum 2 posteriorly with a band of pale pubescence that widens medially to an obtuse angle (Figs. 1, 2, 5) or with a large median spot (Fig. 4); gastral sternum 2 if carinate not ending in a tubercle . . . 3
3. Mid trochanter with narrow apical process (Fig. 12); posterolateral angles of head tuberculate behind eyes (Figs. 14, 15); thorax gently sloping posteriorly, upper margin not dentate nor serrate (Figs. 15, 16); mandible apically with a single tooth (Fig. 6) ..... *Bethsmyrmilla* Krombein and Lelej, new genus
– Mid trochanter without process; posterolateral angle of head not tuberculate but gena tuberculate below eye in *Squamulotilla lamellata* Mickel and *S. arundinacea* Pagden; thorax abruptly sloping posterorly, upper margin usually serrate or dentate, rarely with only an acute median denticle, or if not dentate at all (*S. puerilis* Cameron and *S. afghanica* Lelej) inner mandibular margin with two small preapical denticles (Fig. 9) and gastral tergum 2 with large spot of pale pubescence on posterior margin (Fig. 4) ..... *Squamulotilla* sensu Mickel
4. Apterous; mandible extremely widened apically, with deep preapical emargination; hind coxa ventrally with small, sharp posterolateral denticle; gastral sternum 8 membranous laterally, narrow median part with parallel lateral ridges ..... *Spilomutilla* Ashmead
– Alate; mandible not widened apically, inner border with two small preapical denticles and larger basal one (cf Fig. 9); hind coxa ventrally without denticles; gastral sternum 8 not membranous laterally, with median carina or tubercle; gastral terga 2–5 very often with median longitudinal carina ..... *Squamulotilla* sensu Mickel

Bethsmyrmilla Krombein and Lelej, new genus

(Figs. 1, 6, 10–18)

Type species.—*Bethsmyrmilla alticola* Krombein and Lelej, new species. The genus is monotypic.

Female.—Head large, distinctly wider than thorax, viewed from above the sides gradually widened behind eyes (Fig. 14), widened area forming a sharp tubercle as viewed from behind (Fig. 15); mandible not widened apically, inner margin with subbasal tooth (Fig. 6); medial clypeal lobe with prominent lateral tooth (Fig. 10); flagellomere I 1.8–1.9× its maximal width and 1.8–2.0× as long as flagellomere II (Fig. 11), the latter wider than its length.

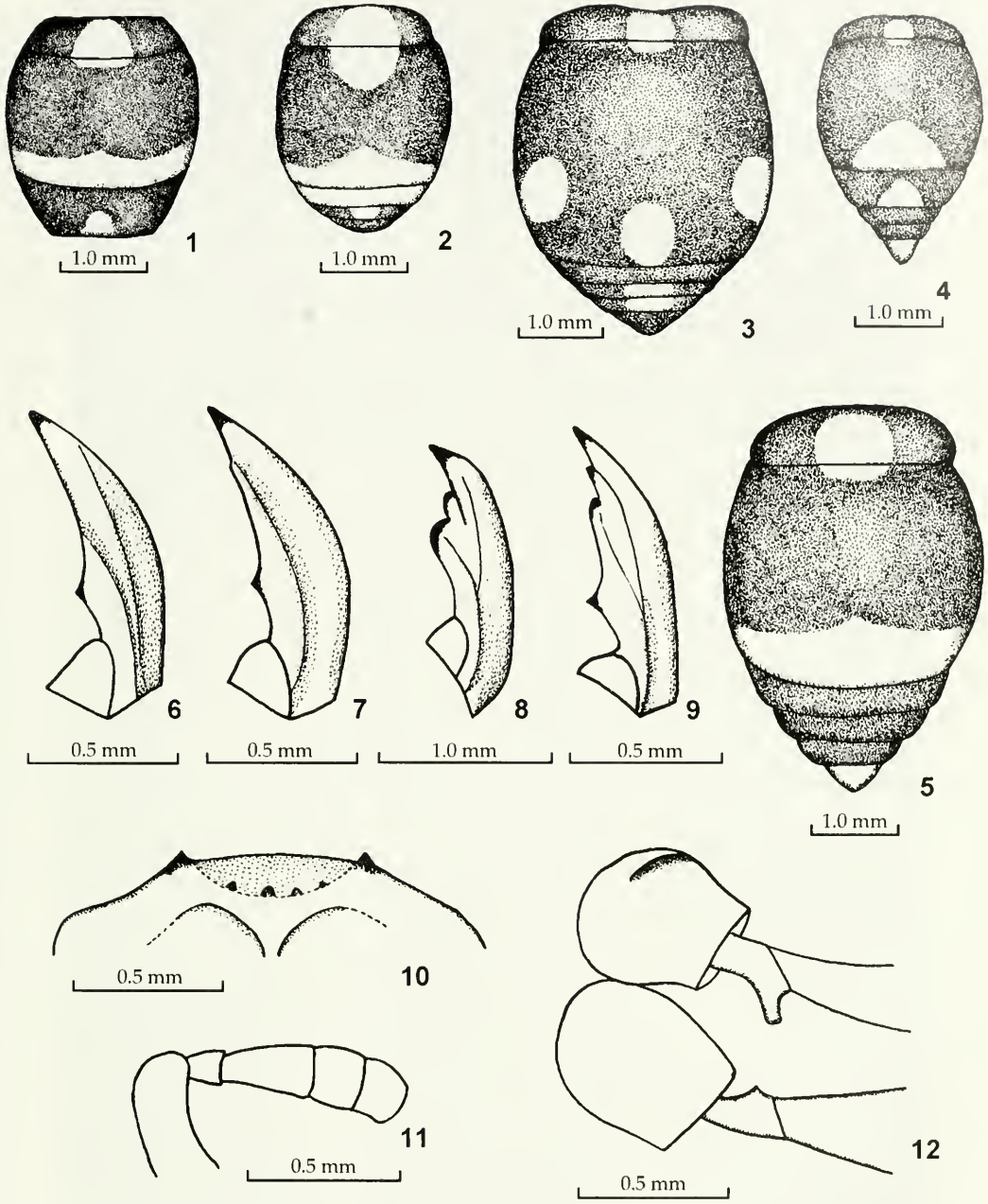
Mesosoma dorsally more or less quadrangular, laterally crenulated (Fig. 15); mesopleuron with trituberculate supracoxal carina (Fig. 16, sc); propodeal dorsum posteriorly without denticles, posterior face of propodeum sloping gently downward; fore tarsi with weak comb (Fig. 18); mid coxa ventrally with blunt tubercle and mid trochanter with narrow apical process (Fig. 12).

Dorsum of gaster with spots and bands of golden pubescence (Fig. 1); basal half of gastral sternum 2 with weak median carina that does not terminate in a tubercle.

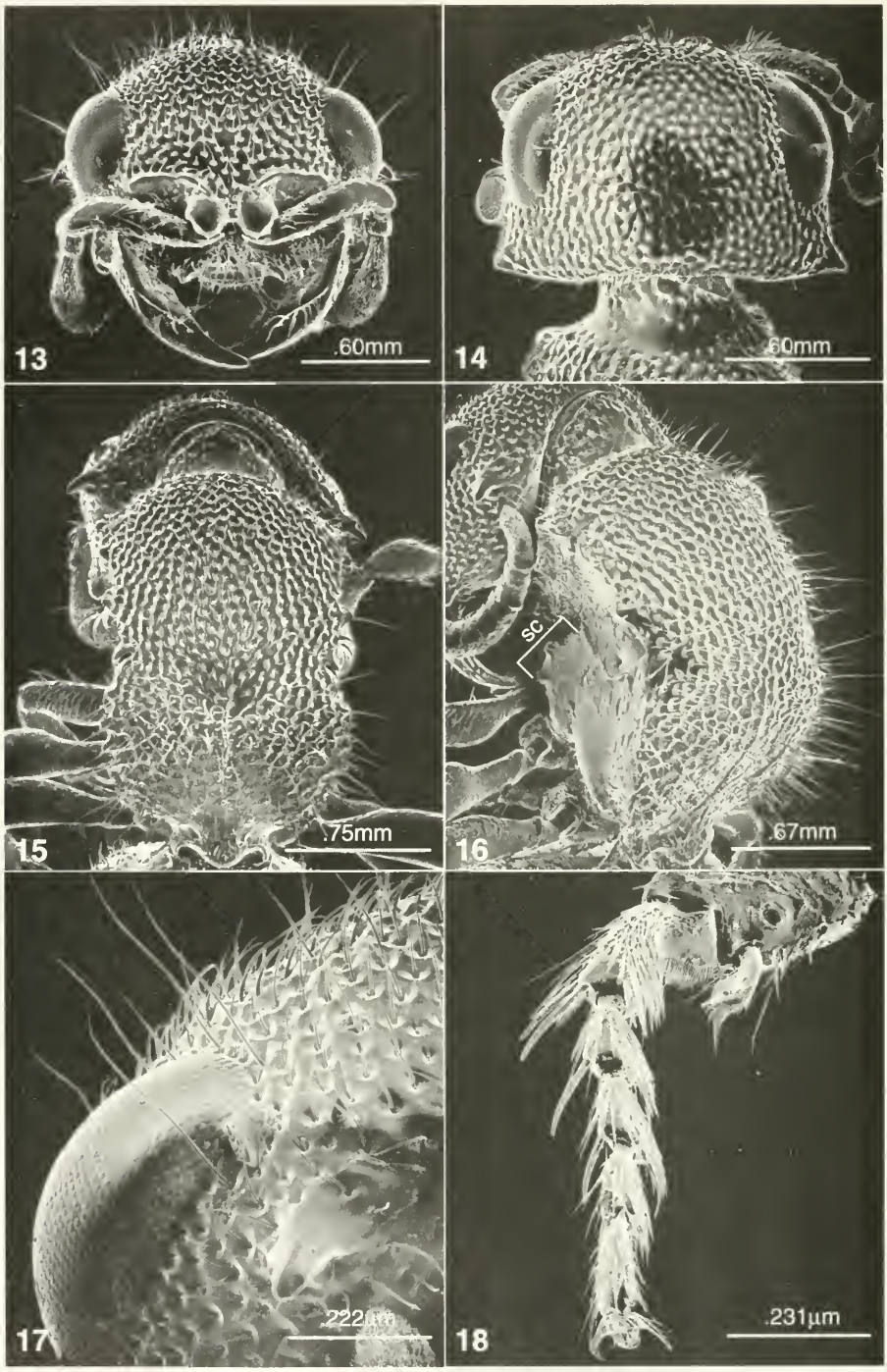
Male.—Unknown.

Discussion.—Differences of this new genus from other Oriental Myrmillinae are noted in the key. The female of *Bethsmyrmilla* is similar to those of *Squamulotilla lamellata* Mickel and *S. arundinacea* Pagden in having a lateral tubercle on the head, similarly shaped mandibles (cf Figs. 6, 7) and similar spots and bands of golden pubescence (cf Figs. 1, 2) on the gaster. It is easily separated from the latter species in lacking a tubercle on the fore coxa, in having a narrow apical process on the mid trochanter and the position of the lateral tubercle on the head, behind the eye in *Bethsmyrmilla* and beneath the eye in the latter two species. Also, the propodeal dorsum in the former is not denticulate posteriorly whereas the latter species have at least an acute median denticle.

The female of *Bethsmyrmilla* is superficially similar to another larger group of *Squamulotilla* species in having spots and bands of golden pubescence on some of the



Figs. 1–12. Females of Oriental Myrmillinae. 1–5, Patterns of pale pubescence on abdominal terga. 1, *Bethsmyrmilla alticola* holotype, Sri Lanka, terga 1–3 only. 2, *Squamulotilla lamellata*, Vietnam. 3, *Spilomutilla consolidata* (Cameron), Sri Lanka. 4, *Sq. puerilis*, South India. 5, *Sq. strangulata* (Smith), South China. 6–9, Mandible. 6, *B. alticola*. 7, *Sq. lamellata*. 8, *S. consolidata*. 9, *Sq. puerilis*. 10–12, *B. alticola*. 10, Clypeus, frontal view. 11, Antennal segments 1–5. 12, Coxa, trochanter, base of femur, mid leg above, hind leg below.



Figs. 13–18. *Bethsmyrmilla alticola*, female paratype uncoated. 13, 14, Head. 13, Frontal view (note genal tubercle extending laterad of each eye on lower margin). 14, Dorsal view. 15, 16, Thorax. 15, Dorsal view. 16, Oblique view, bracket and sc indicate supracoxal carina. 17, Head, posterolateral view, note sparse, long setae that margin eye. 18, Foretarsus, note that basal segment is angled, foreshortened.

gastral terga but differs markedly in having the lateral tubercle on the head, in lacking denticles along the posterior margin of the thoracic dorsum and in the gently rather than abruptly sloping posterior surface of the thorax.

Etymology.—We take great pleasure in naming this remarkable mutillid for Beth B. Norden, collector of the type series of *B. alticola* and discoverer of its probable host species.

Bethsmyrmilla alticola Krombein and Lelej, new species

(Figs. 1, 6, 10–18)

Female.—Length (through gastral segment 3) 5.0 mm. Red; gaster black except sternum 1 totally and tergum 1 basally red; mandible red, brownish apically; palpi brownish; scape red, flagellomeres red, darkened above; legs red, mid and hind tibiae with darker spines; mandible and clypeus with long pale erect setae, scape with shorter ones; frons and vertex with sparse recumbent, short reddish setae, genae with whitish ones; vertex and frons along eye orbit with sparse, long, erect black setae (Fig. 17); thoracic dorsum with sparse, short, subappressed black setae mixed with long, erect black ones; legs with subappressed and erect yellowish setae; pattern of golden pubescence on gaster (Fig. 1); gastral sterna 2 and 3 posteriorly with whitish fascia; propodeal hindface, gastral tergum 1 anteriorly, gastral sternum 2 and gastral terga 2 and 3 laterally with sparse, erect, whitish setae.

Head parallel behind eyes, gena posterolaterally with strong acute tubercle (Figs. 13–17); antennal scrobe well developed between antennal tubercle and lower part of eye (Fig. 13); clypeus delimited above by a weak convex carina with four small tubercles and ending laterally in a strong tooth (Figs. 10, 13); antenna with short flagellomeres (Fig. 11), flagellomere I 1.8–1.9× its apical width and 1.8–2.0× flagellomere II, the latter 0.75× its width; hypostomal carina without projection; gena below not carinate; head above with dense large punctures (Figs. 13, 14, 17). Thorax viewed from above (Fig. 15) more or less quadrangular with slightly widened pronotal and propodeal areas; humeral angles developed, lateral margin of pronotum with vertical ridge (Fig. 16); thoracic dorsum noticeably convex, weakly serrate laterally, with one lateral tubercle on the middle of mesonotum, and with dense reticulate punctures; propodeal dorsum posteriorly not dentate nor serrate; mesopleuron concave with supracoxal carina well developed, the latter with three blunt tubercles (Fig. 16, sc); mid coxa ventrally with blunt tubercle and mid trochanter with narrow apical process (Fig. 12); hind coxa carinate along posterior margin of ventral surface, carina ending in a blunt tubercle.

Gastral sternum 1 with well developed median carina; gastral tergum 2 with rather short lateral felt line and dense small punctures; gastral sternum 2 with more or less flattened central disc and dense punctures which are much sparser and larger on disc; gastral segments 4–6 lacking in holotype and 3–6 in paratype (these parts accidentally amputated and lost during nest digging).

Male.—Unknown.

Range.—The species is known only from a trail at about 1,950 m altitude along the upper border of the Hakgala Botanic Garden about 10 km S of Nuwara Eliya. We believe that it may be more widely distributed. Its probable host has been collected only at high altitudes, 1,700–1,950 m, at various localities in the districts of Nuwara Eliya (Nuwara Eliya, Hakgala, Horton Plains) and Kandy (Adam's Peak Trail).

Type material.—Holotype ♀, Sri Lanka, Nuwara Eliya District, Hakgala Botanical Garden, 6°55′N, 80°49′E, 21–22 April 1997, B.B. Norden [USNM]. Paratype ♀, same data as holotype but 24–26 February 1997 [IBPV].

Etymology.—The specific name is from the Latin *altus,* high, and *-cola,* dweller.

Natural history.—Beth Norden excavated two nests of *Lasioglossum (Sudila) alphe-*

num one each on 26 February and 22 April 1997. Each nest contained a single female mutillid. Both wasps were found at the bases of the nest tunnels and are presumed to have traveled to the farthest reaches of the vertical shafts in an effort to avoid capture.

The February nest shaft reached a depth of 7 cm and also contained a female *L. alphenum* and a female of the parasitic bee *Nomada priscilla* Nurse that were captured a few mm above the mutillid. The April nest shaft reached a depth of 13 cm. In this nest, two female *L. alphenum* were collected at depths of 12 and 12.5 cm respectively.

The mutillids moved more vigorously than the bees and were more difficult to collect. Pollen and immature bees (larvae and pupae in various stages of development) were found in cells located above the base of the nest where the wasps were retrieved.

Discussion.—Norden et al. (1994) found two females of the mutillid wasp *Pseudomethoca bethae* Krombein within a communal nest of an Arizona bee *Exomalopsis (Phanamalopsis) solani* Cockerell. One mutillid was within a provisioned cell presumably to feed on the pollen-nectar mass. Although neither specimen of *B. alticola* was in a cell with provisions, we suspect that they would use this convenient source of food while they remained within the nest. And when bee brood reached the appropriate developmental stage it would be available for parasitism. Such cryptic behavior by the mutillid would greatly lessen exposure to predators and may explain the rarity of this species in collections.

Acknowledgments

Within the Smithsonian Institution we thank Beth B. Norden for her notes on the natural history of *B. alticola* and preparing specimens for SEM study, Susann G. Braden for skillful preparation of the scanning electron micrographs and George L. Venable for preparation of the plates. We are grateful to P. Klimov (IBPV) for preparing Figures 1–12. ASL thanks the late Borge Petersen for generously providing valuable exchange material of Oriental mutillid wasps and V. Kuznetsov (IBPV) for the gift of material. KVK thanks Bryan N. Danforth, Cornell University, Ithaca, NY, for identification of *Lasioglossum (Sudila) alphenum* and Maximilian Schwarz, Ansfelden, Austria, for identification of *Nomada priscilla*. We are grateful to G. Nonveiller, Zemun, Yugoslavia, for critical reading of the manuscript and valuable comments, and also an anonymous reviewer.

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TWO NEW WESTERN NEARCTIC *CULICOIDES* LATREILLE (DIPTERA: CERATOPOGONIDAE) DESCRIBED FROM ALL STAGES

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Abstract.—The egg, larva, pupa, and adult of two new species of *Culicoides* Latreille from desert mountains in southern California and Baja, Mexico are described: ***C. kettlei*** and ***C. vetustus***. Descriptions of immatures were made from laboratory-reared material. Rearing techniques and notes on behavior observed in the laboratory are presented.

Key Words: *Culicoides*, Ceratopogonidae, immatures, morphology

Bluetongue and epizootic hemorrhagic disease viruses have been suspected of contributing to lamb mortality in desert bighorn sheep populations in southern California (DeForge et al. 1982, Wehausen et al. 1987, Elliott et al. 1994). A comprehensive survey of potential vectors (*Culicoides* Latreille) occurring in bighorn habitats within the desert mountains of southern California (Mullens and Dada 1992a) revealed three undescribed species of *Culicoides*. The adults of one species, *Culicoides boydi* Wirth and Mullens have been previously described (Wirth and Mullens 1992). The present study describes all life-stages of these remaining two species and provides data on their biology and geographic distribution.

MATERIALS AND METHODS

Host-seeking females were collected using suction traps baited with 1 kg of dry ice. Some females collected at the Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, Riverside Co., CA, or near the town of Morongo Valley, San Bernardino Co., were given the opportunity to feed on heated, defibrinated sheep blood through a parafilm or chick-skin membrane (Hunt 1994). Engorged females were separated from other midges in the collections while they were immobilized on a chill table. Female midges were then held at 21°C for 7 days. Some individual females would oviposit onto damp filter paper, when held overnight in a petri dish. Gravid females which did not oviposit were decapitated to induce oviposition.

Filter paper with eggs from an individual female was placed in a petri dish containing nutrient-enriched 1.5% noble agar. Eggs were held in a humid chamber and checked daily for hatch. First-instar larvae were offered several food sources, including a nutrient rich liquid diet consisting of bacteria, algae, and yeast used for rearing colonized *Culicoides variipennis sonorensis* Wirth and Jones (Jones et al. 1969). In addition, the bacterial feeding nematodes, *Pelodera* sp. and *Panagrellus redivivus* (L.), were supplied as potential prey on a biweekly basis (Mullens and Velten 1994). Larval growth and feeding behavior were observed daily and the duration of egg, larval, and pupal development recorded.

Samples of eggs from associated females

were placed into 70% EtOH. Specimens were fixed (Day et al. 1997), then critical-point dried, transferred onto stubs backed with sticky tape, sputter-coated with gold-palladium, and viewed on either a JOEL JSM-35C or Phillips XL30 scanning electron microscope.

The parental adult female was preserved in 70% EtOH and slide-mounted in balsam after Wirth and Marston (1968). Fourth-instar larvae, pupae, and adults from reared offspring of the parental female were also preserved. Offspring were mounted in Canada balsam or Hoyer's medium. Descriptions of immature stages and males of both species were made from laboratory-reared material.

The terminology of Downes and Wirth (1981) is used for adults, of Lamberson et al. (1992) and Nevill and Dyce (1994) for pupae, of Murphree and Mullen (1991) for larvae, and of Becker (1961) and Campbell and Kettle (1975) for eggs. Nomenclature agrees with Borkent and Wirth (1997) and Spinelli and Ronderos (1997).

The following measurements were made from fourth-instar larvae: total length (TL), head length (HL), head width (HW), subgenal width (SGW), mandible length (ML), width across the lateral arms of the epipharynx (LAW), total width across the paired dorsal comb sclerites of the epipharynx (DCW), caudal-segment length (CSL), caudal-segment width (CSW), length of setae 'o' (OL), and the distance between their bases.

From values listed above, the following ratios were calculated: head ratio (HR = HL/HW), subgenal ratio (SGR = HW/SGW), and caudal-segment ratio (CSR = CSL/CSW). Illustrations were made of the morphology and chaetotaxy of the head capsule and caudal segment. The hypostoma, epipharynx, hypopharynx, and mandible were illustrated, and thoracic pigmentation and anal papillae were drawn when appropriate.

For pupae the following structures were described and illustrated: respiratory horn, operculum, caudal segment, and the *ad, dl, dasm, dpm, lasm, lpm,* and *vpm* tubercles.

The holotype, allotype, and some paratypes are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC; paratypes, as available, will be deposited in the collections of the University of California, Riverside and the California Academy of Sciences, San Francisco.

Culicoides (Haematomyidium) kettlei Breidenbaugh and Mullens, new species

(Figs. 1–4)

Egg.—Banana-shaped. Surface with two types of ansulae arranged in longitudinal rows (Fig. 1A). Moderately stalked ansulae present on concave surface, ridges composed of flattened papillate ansulae on convex surface (Fig. 1B). Average length = 356 ± 17 μ; width = 53 ± 2 μ (n = 11).

Larva.—Total length = 2.79 (2.16–3.51, n = 15) mm. *Head capsule* (Figs. 2A–C): Light brown. Small larvae, HL = 128 (122–134, n = 29) μ, HW = 89 (82–102, n = 28) μ; shape somewhat long and narrow, SGW = 58 (54–67, n = 30) μ; HR = 1.4 (1.2–1.6, n = 27); SGR = 1.5 (1.4–1.8, n = 27). Mandible (Fig. 2F) medium-small, ML = 35 (22–38, n = 29) μ; with pointed apex and subapical rounded prominence; base with distinct point of articulation. Hypostoma (Fig. 2G) rounded, entire. Labium small, crescent-shaped and sclerotized. *Epipharynx* (Fig. 2H): Dorsal-comb sclerites with 5–7 unequal angular teeth; moderately-wide, DCW = 11 (10–13, n = 17) μ. Comb 2 narrow with short, rounded teeth; comb 4 wider, with rounded teeth. LAW = 49 (43–52, n = 30) μ; lateral curtains composed of short, dense, filamentous processes. Hypopharynx apparently poorly sclerotized, not seen. *Thoracic pigmentation* (Fig. 2I): distinct lateral pattern on thoracic segments. Prothorax with arched pattern; mesothorax and metathorax with crescent and sagittate patterns, respectively. *Caudal segment* (Figs. 2D, E): Short, CSL = 231 (189–285, n = 32) μ and moderately-wide, CSW = 126

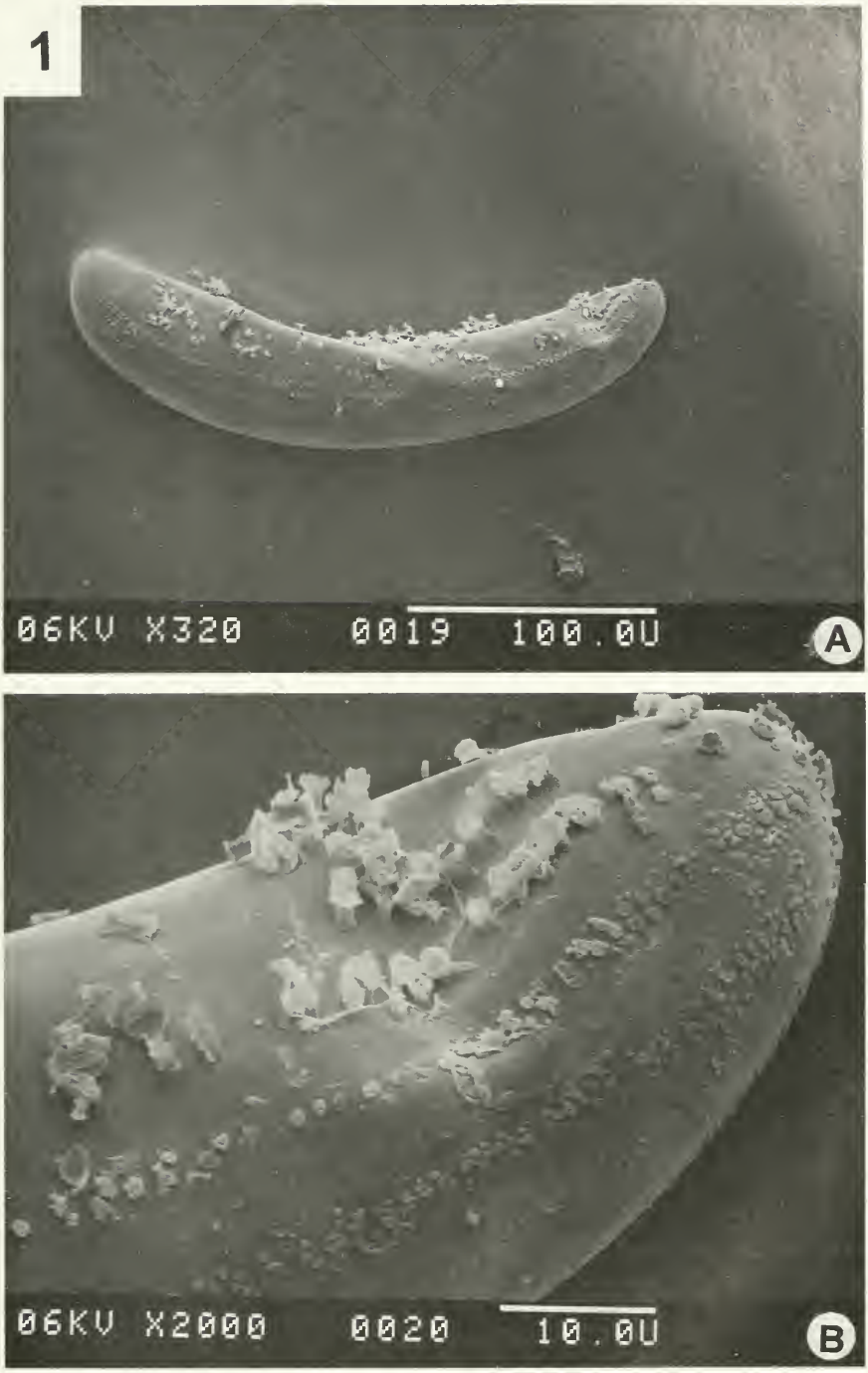

Fig. 1. *Culicoides kettlei*, egg. A, Lateral view. B, Detail of surface.

(90–179, n = 31) μ; Oval; CSR = 1.9 (1.5–2.2, n = 31). Setae "o" short relative to the CSL, OL = 46 (38–51, n = 19) μ; bases of setae moderately separated, OD = 37 (26–45, n = 19) μ. Anal papillae not observed.

Material studied.—Laboratory-reared from

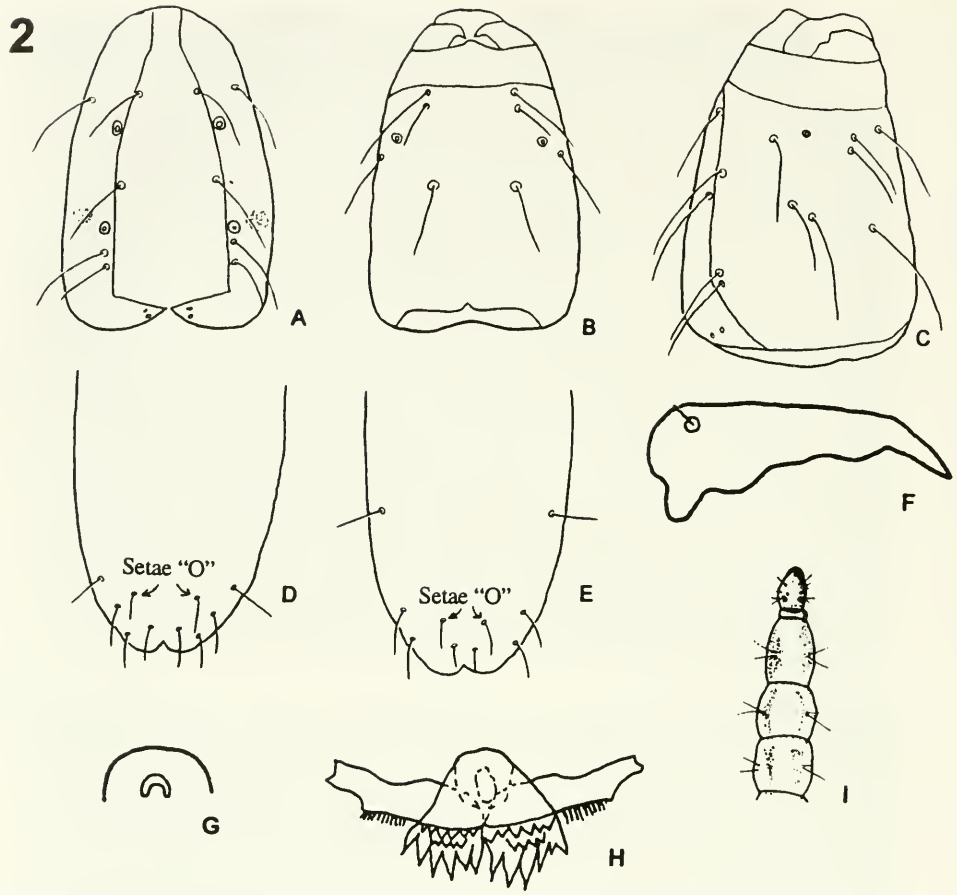

Fig. 2. *Culicoides kettlei*, larva. A–C, Head capsule. A, Dorsal view. B, Ventral view. C, Lateral view. D, Caudal segment, dorsal view. E, Caudal segment, ventral view. F, Mandible. G, Hypostoma. H, Epipharynx. I, Thoracic pigmentation, dorsal view.

eggs deposited by individual females collected in San Bernardino County, CA, Morongo Valley, 15-VI-95 (n = 3); 22-V-96 (n = 5); 14-VI-96 (n = 24), paratypes: slides 25,26,27.

Pupa.—Light yellow brown. *Respiratory horn* (Fig. 3A): yellow brown; basal half crenulated; spines, sparsely distributed. Four lateral spiracules present and 8–11 apical spiracles. Tracheal annulations associated with tracheae visible in basal portion and a reticulated pattern is visible in distal portion. *Operculum* (Fig. 3B): Yellow brown, with two types of spines, neither extending beyond the *am* tubercles. Sagittate spines occurring laterally; smaller, rounded spines occurring medially. Anterior margin moderately notched. *Caudal segment* (Fig. 3C): Spines present at base of posterolateral processes, absent apically; band of spines along anterior margin and a patch of spines located basimedially on dorsum.

Chaetotaxy: Dorsal tubercles (Fig. 3D): 1 and 2 round with stout spine; 3 round with a short seta; 4 a slender seta; 5 a small, round pore. *ad* tubercle (Fig. 3E): spinate with two subequal spines. *dl* tubercle (Fig. 3F): with 3 unequal, slender spines. Abdomen (Fig. 3G): *dasm* tubercles: 1 with a spine and 2 a bristle. *dpm* tubercles: rounded; 1 and 2 with short spine; 3 and 4 lack setae; 5 with a short hair. *lasm* tubercle: spi-

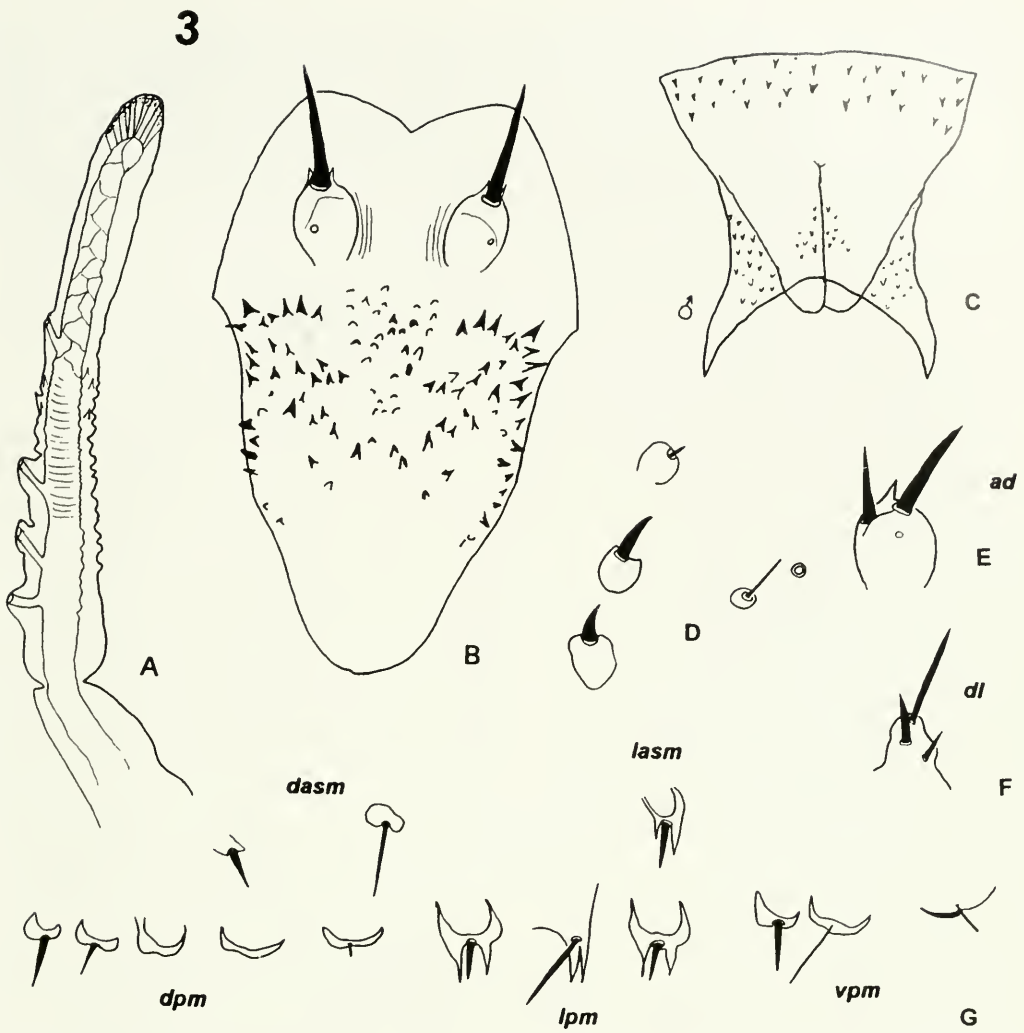

Fig. 3. *Culicoides kettlei,* pupa. A, Respiratory horn. B, Operculum. C, Caudal segment. D, Dorsal tubercles. E, ad tubercle. F, dl tubercle. G, Abdominal chaetotaxy.

nate with short spine. *lpm* tubercles: 1–3 spinate; 1 and 3 with short spine; 2 with a bristle. *vpm* tubercles: rounded; 1 with a spine; 2 and 3 with long and medium length setae, respectively.

Material studied.—Laboratory-reared from individual females collected in San Bernardino County, CA, Morongo Valley, 14-V-95 (n = 6), paratypes: slides 10,11.

Adults.—Female: Wing length 1.06 (0.92–1.19, n = 28) mm. *Head:* Eyes (Fig. 4A) bare; separated by a single facet width; without interfacetal hairs. Antenna (Fig. 4B) with lengths of flagellomeres of holotype 43-27-28-33-29-31-30-33-36-37-43-47-63 (in μ); antennal ratio 0.91 (0.74–1.04, n = 28); well-developed sensilla coeloconica present on flagellomeres 1, 4–8; 26% (7/27) of observed specimens lack sensilla on flagellomere 4. Palpus (Fig. 4C) with lengths of segments 24-46-61-20-26; palpal ratio 2.07 (1.75–2.36, n = 29); P/H ratio 0.79 (0.70–0.86, n = 18); third segment swollen with broad shallow sensory pit. *Thorax:* Brown, scutum without conspicuous pattern. Legs brown (Fig. 4D),

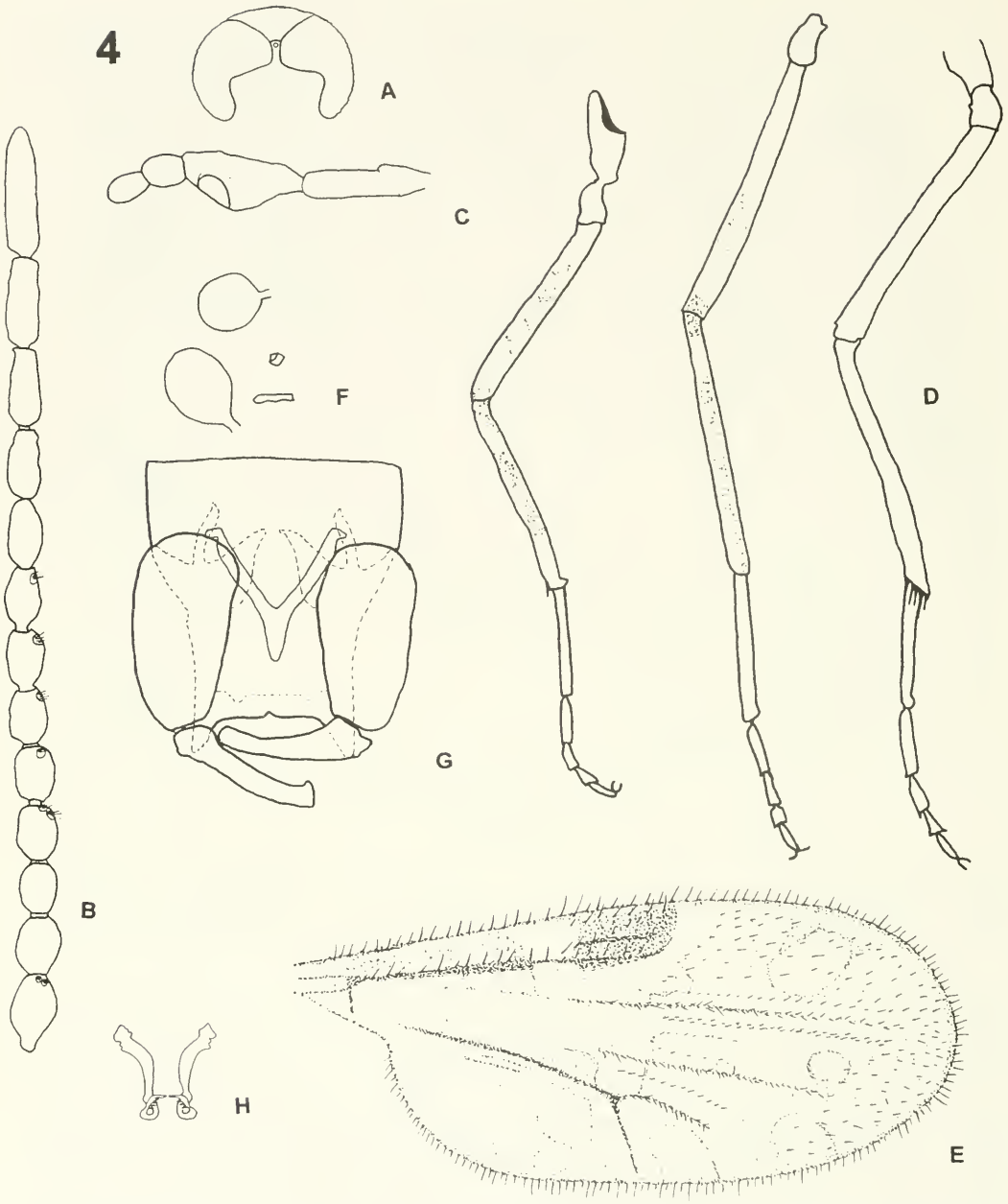

Fig. 4. *Culicoides kettlei*, adult. A–F, Female. G–H, Male. A, Eye separation. B, Antenna. C, Palpus. D, Legs, left to right, front, mid, and hind. E, Wing. F, Spermathecae. G, Genitalia, parameres omitted. H, Parameres.

femorotibial joints blackish; fore and mid femora with narrow subapical pale rings, all tibiae with narrow subbasal pale rings and hind tibiae with distal fourth pale; hind tibial comb with five spines, second from the spur longest. Wing (Fig. 4E) with a slightly angular poststigmatic pale spot; distinct transverse pale spot present in r5; cell m1 with narrow pale spot; cell m2 with rounded pale spot located distally and with a longitudinal pale spot lying posterior to medial fork. Macrotrichia in moderate numbers

evenly distributed over wing. Halter pale. *Abdomen:* Brown. Two slightly unequal spermathecae, plus rudimentary third and sclerotized ring (Fig. 4F). Functional spermathecae with long slender necks; length, including neck, 32 (29–37, n = 25) μ for the larger, 29 (26–35, n = 26) μ for the smaller.

Male: *Genitalia* (Figs. 4G–H): Ninth sternum with scarcely perceptible caudomedian excavation, ventral membrane spiculate; apicolateral processes moderately long, pointed, caudal margin between them slightly cleft medially. Gonocoxite moderately stout; ventral root with anterior point longer, more slender than dorsal root; gonostylus moderately curved and slender with moderately bent, pointed tip. Aedeagus with basal arch extending more than two-thirds of total length; distal portion short, tapering to a simple tip. Paramere (Fig. 4H) with strong basal knob; midsection arched; distally, greatly narrowed and reflexed upon midsection, constricting to a noticeably fringed filamentous tip.

Distribution.—Southern California and northern Baja California, Mexico.

Material studied.—HOLOTYPE: ♀, Riverside County, CA, Deep Canyon, Bighorn Overlook, nr. Palm Desert, 22-IX-88 (B. A. Mullens), CO_2-baited trap. ALLOTYPE: ♂, San Bernardino County, CA, Big Morongo Canyon, Morongo Valley, 15-VI-95 (Breidenbaugh), laboratory-reared from wild-collected female. PARATYPES: CALIFORNIA. 6 ♀, same data as holotype, except 1 ♀ 24 May 1988; 6 ♀, Riverside Co., Bighorn Drive, Palm Desert, 8 October 1988, CO_2-baited trap, 1 ♀, same except 22 September 1988; 9 ♀, 4 ♂, same data as allotype except from June 1995 to July 1996 (some K. Luhring); MEXICO. 7 ♀, Mexico, Baja California, Cadavina, 19 March 1994 (C. Szijj), CO_2-baited trap.

Behavior and rearing.—In the laboratory, the average female fecundity was 74 ± 24 eggs (n = 10). From a single reared cohort observed daily, pupation first occurred 26 days following egg hatch. In culture, larvae fed on *Pelodera* sp. nematodes. Adults have been collected from soil-emergence traps along a seasonal creek in the Deep Canyon watershed (Breidenbaugh and Mullens, in preparation), indicating that creek margins are used by this species as a larval development site. Feeding behavior is poorly known with a single report of an unfed female recovered from a bighorn sheep (Mullens and Dada 1992b).

Discussion.—*Culicoides kettlei,* was originally recognized by the late W. W. Wirth who referred to this species as #120 (W. W. Wirth, personal communication). Following Vargas (1960) the male genitalia fit nicely into the subgenus *Haematomyidium.* The female wing pattern is inconclusive, since the r-m crossvein is not dark. However, we feel that placement in the subgenus *Haematomyidium* is reasonable. Adult morphology is similar to that of *Culicoides* (*Haematomyidium*) *debilipalpis* Lutz, a common biting midge in the eastern U.S.. From 1985–1997 *C. debilipalpis* was synomized with *C. lahillei* Iches (Spinelli and Wirth 1985). Recently, however, the validity of *C. debilipalpis* was confirmed (Spinelli and Ronderos 1997). The range of *C. debilipalpis* includes the southeastern U.S. as far west as Louisiana, with a disjunct distribution that includes Costa Rica south to Argentina. In contrast, *C. lahillei* is strictly South American. The females of *C. kettlei* can be easily separated from *C. debilipalpis* and all other Nearctic members of *Haematomyidium* by the antennal sensorial pattern (1,4(5)-8) (Wirth et al. 1985). In addition, no Neotropical species of *Haematomyidium* are known to occur north of southern Mexico (Wirth et al. 1988), and their range thus does not overlap with that of *C. kettlei.*

Apart from the similarity in size, the larvae of this species are noticeably different from those of the only other North American species in this subgenus with described larvae, *Culicoides paraensis* (Goeldi)(Murphree and Mullen 1991). The hypostoma is round and smooth in this species

while lateral teeth are present in *C. paraensis*. Furthermore, the hypostoma lacks the distinct subapical notch seen in *C. paraensis*. The pupa of this species is similar to *C. paraensis* in the type and location of spines on the operculum.

Etymology.—This species is named in honor of Dr. D. S. Kettle, Emeritus Professor, Department of Entomology, University of Queensland, Australia, for his pioneering work on the biology of *Culicoides*, specifically in the discipline of the morphology of immatures.

Culicoides vetustus Breidenbaugh and Mullens, new species

(Figs. 5–8)

Egg.—Cigar-shaped. Surface with flattened longitudinal rows, many not contiguous from end to end (Fig. 5A). Ansulae flattened, not distinct, merge to form longitudinal ridges (Fig. 5B), present on all lateral surfaces, and not varying with curvature. Average length = 267 ± 28 μ and width = 49 ± 3 μ (n = 8).

Larva.—Total length = 3.25 (2.81–4.0, n = 15) mm. *Head capsule* (Figs. 6A–C): Yellow; medium sized, HL = 180 (166–192, n = 28) μ, HW = 123 (109–138, n = 27) μ, SGW = 90 (80–102, n = 28) μ; overall shape long and narrow, HR = 1.5 (1.2–1.7, n = 27), very oblong, SGR = 1.4 (1.2–1.5, n = 27). Mandible (Fig. 6D) medium length, ML = 51 (48–54, n = 24) μ; base wide; pointed marginal prominence basimedially, followed by a subapical notch, sharply angled to pointed apex. Hypostoma (Fig. 6E) difficult to see but rounded medially and smooth. *Epipharynx* (Fig. 6F): Dorsal-comb sclerites moderately wide, DCW = 14 (13–15, n = 24) μ, with 5 subequal pointed teeth/sclerite; comb 4 with many unequal pointed, rounded teeth; lateral curtains wide; teeth thin, hair-like; LAW wide relative to DCW, LAW = 60 (52–67, n = 21) μ, indented near lateral apex. Hypopharynx (Fig. 6G) with hypopharyngeal fringe separated into two distinct prominences by a medial notch. *Thoracic pigmentation* (Fig. 6H): Absent. *Caudal segment:* Short with length varying considerably among individuals, CSL = 286 (131–326, n = 25) μ; narrow, CSW = 139 (86–157, n = 26) μ, CSR = 2.1 (1.5–2.4, n = 25); setae "o" of medium length, OL = 82 (61–99, n = 18) μ, and well separated, OD = 45 (35–53, n = 21) μ. Anal papillae (Fig. 6I) four deeply bifurcate pairs.

Material studied.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, CA, Morongo Valley, 15-VI-95 (n = 6); 14-V-96 (n = 15); 14-V-96 A42 (n = 15), paratypes: slides 2–7.

Pupa.—Light to dark brown. *Respiratory horn* (Fig. 7A): Proximal portion light brown; roughly divided into 3 subequal portions. First section with annular tracheae; second portion annulations obscured by reticulation pattern; 3 lateral spiracular protuberances present; terminal section, dark brown with 5–9 spiracular openings apically; few scales on horn. *Operculum* (Fig. 7B): Mostly smooth, 3–8 large spines on lateral margins and patch of setae on central portion; no large spines medial to the *am* tubercles; large spines triangular. *Caudal segment* (Figs. 7C–D): Narrow V-shaped cluster of small spines on dorsal surface of both sexes. Anterior band of spines complete on both sexes; large spines on proximal ⅔ of posterolateral processes; distal third, smooth dark brown.

Chaetotaxy: Dorsal tubercles (Fig. 7E): setae 1 and 2 of medium length, stout; seta 3 short, stout; seta 4 a long, slender bristle; 5 a circular pore. *ad* tubercle (Fig. 7F) with one long, one shorter setae. *dl* tubercle (Fig. 7G) with a long slender bristle and second shorter thicker bristle. Abdomen (Fig. 7H): *dasm* tubercles: setae 1 and 2 of medium thickness, 1 longer than 2. *dpm* tubercles: setae 1 and 2 equal; 3 and 4 lack setae; 5 short. *lasm* tubercle: rounded with short spine. *lpm* tubercles: spinate with shorter, stouter, equal bristles on 1 and 3, bristle 2 longer and slender. *vpm* tubercles: 2 with a

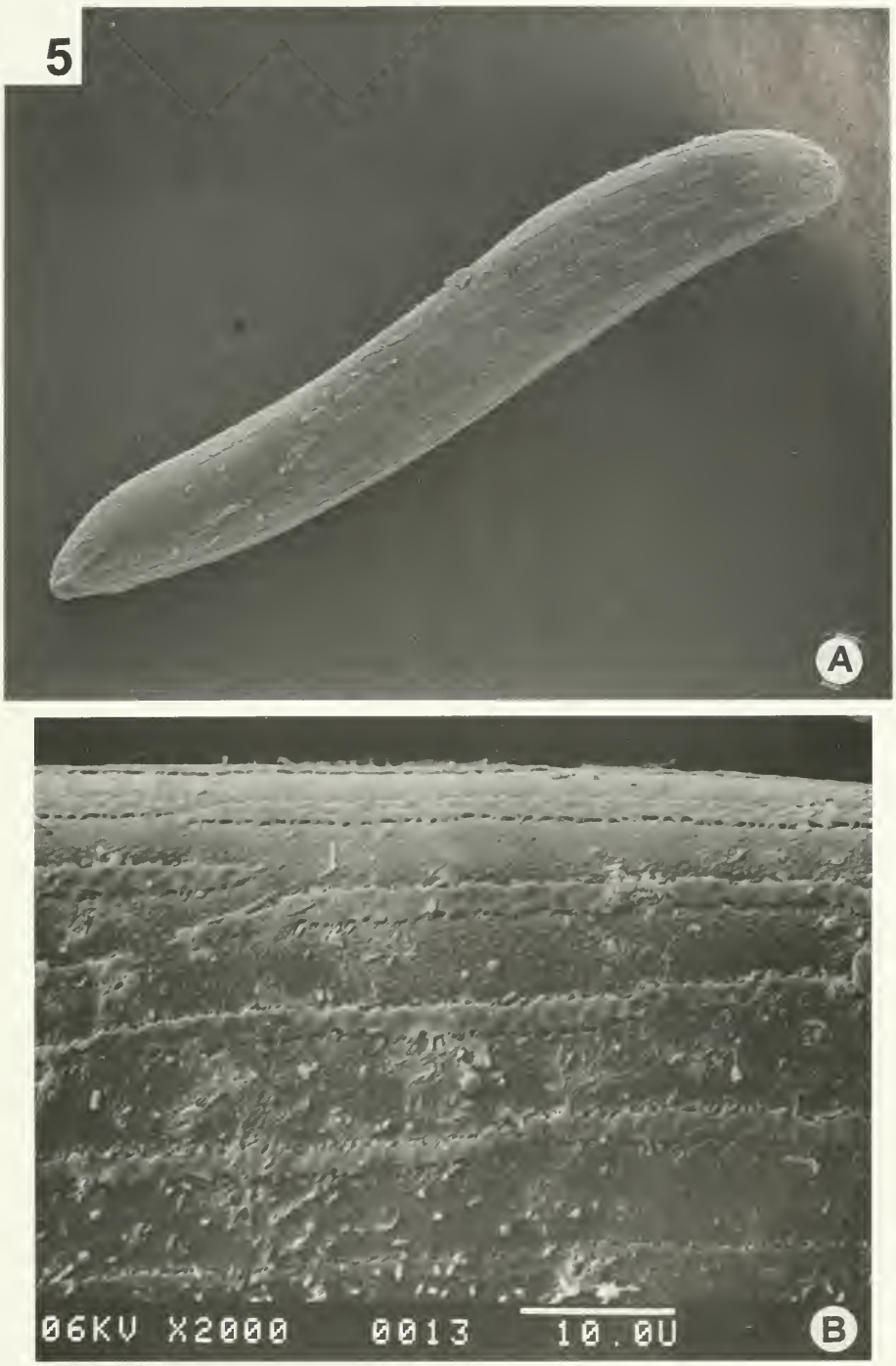

Fig. 5. *Culicoides vetustus*, egg. A, Lateral view of entire egg. B, Detail of egg surface.

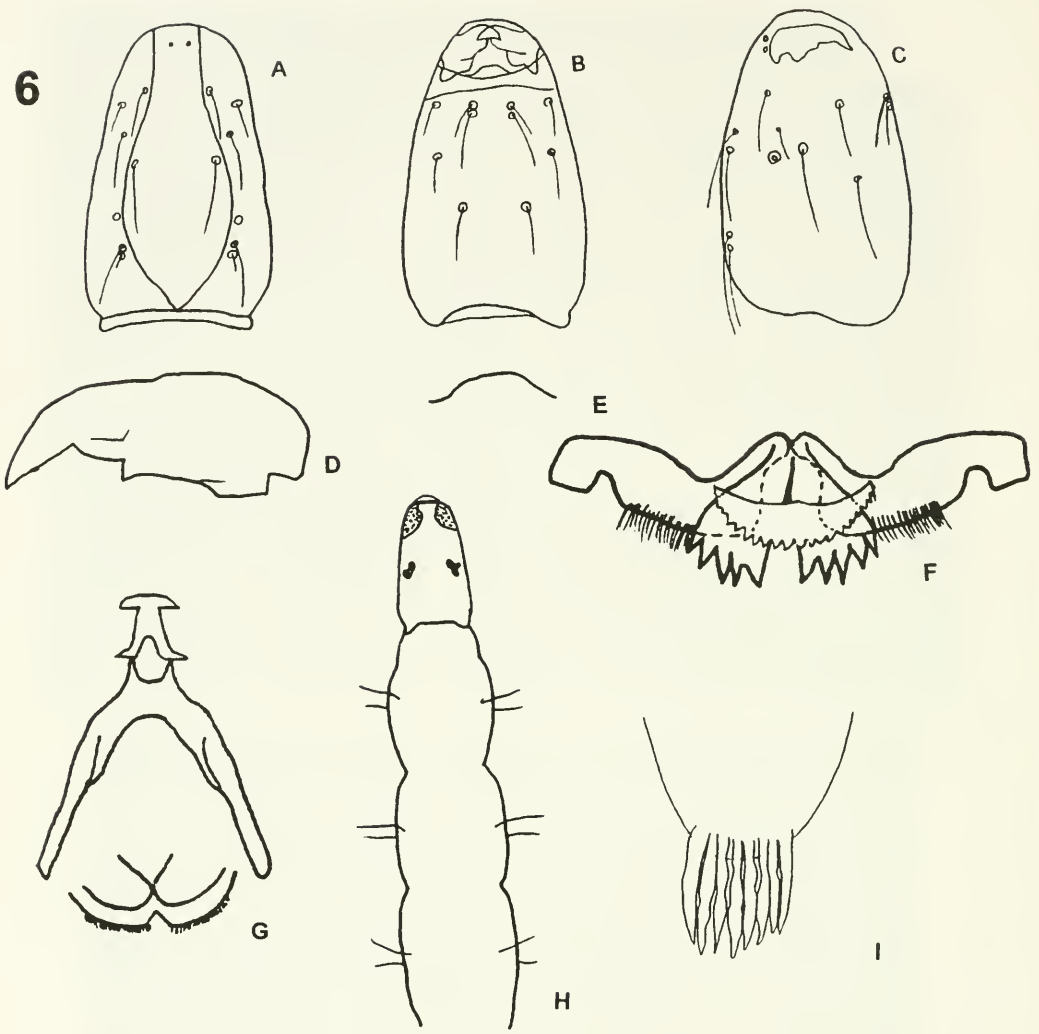

Fig. 6. *Culicoides vetustus*, larva. A–C, Head capsule. A, Dorsal view. B, Ventral view. C, Lateral view. D, Mandible. E, Hypostoma. F, Epipharynx. G, Hypopharynx. H, Head and thorax, dorsal view. I, Anal papillae, caudal segment.

slender bristle, longer and thinner than 1 and 3.

Material examined.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, CA, Morongo Valley, 14-V-96 (n = 8); 15-VI-95 A5 (n = 17), paratypes: slides 17–18; 14-V-96 A42 (n = 3), paratypes: slide 1.

Adults.—Female: Wing length 1.24 (1.1–1.4, n = 20) mm. *Head:* Eyes (Fig. 8A) separated by single facet width; without interfacetal hairs. Antenna (Fig. 8B) lengths of flagellomeres of holotype 46-28-28-30-30-30-33-33-43-46-46-50-65; antennal ratio 0.97 (0.92–1.0, n = 18); well-developed sensilla coeloconica present on flagellomeres 1, 11–13. Palpus (Fig. 8C) with lengths of segments 24-50-78-30-33; third segment swollen, with round moderately deep sensory pit near apex. Palpal ratio 2.06 (1.8–2.3, n = 21); proboscis long, P/H ratio 0.95 (0.81–1.3, n = 19). *Thorax:* Brown, lateral aspects of scutum darker. Legs brown, lacking pattern; hind tibial

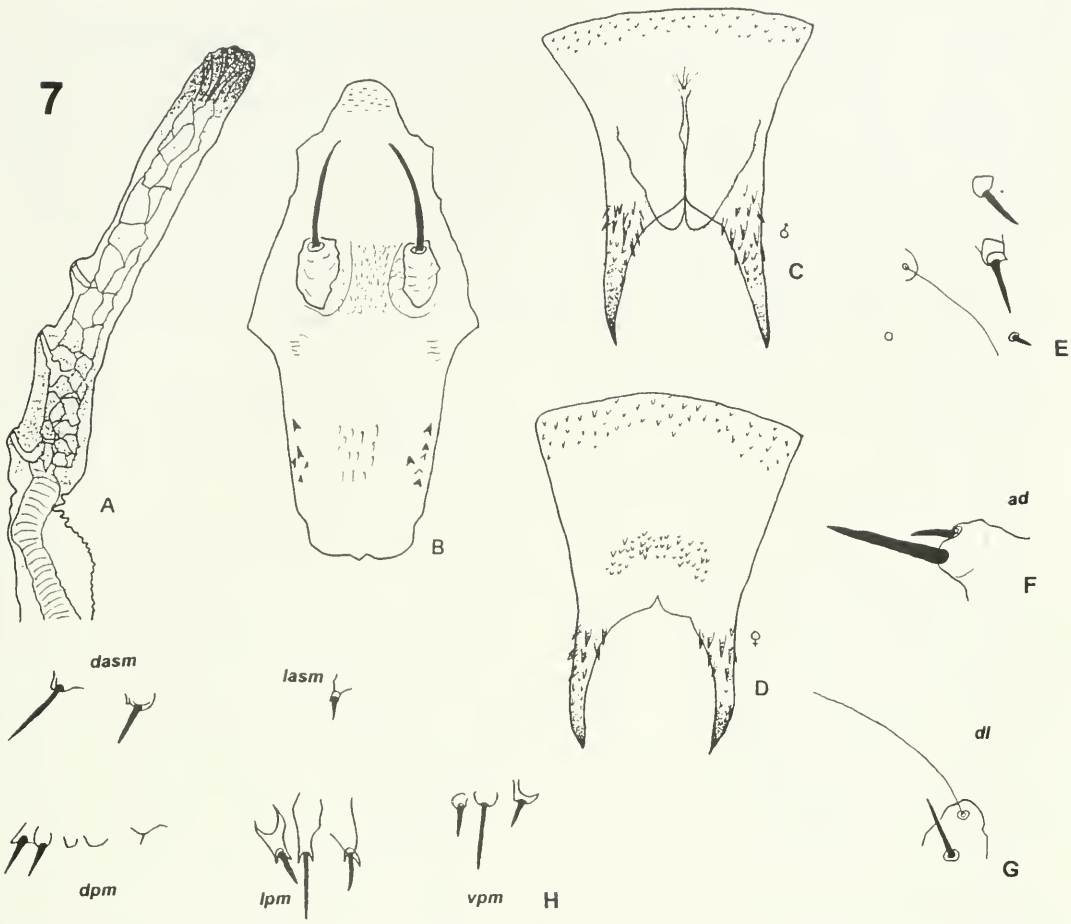

Fig. 7. *Culicoides vetustus*, pupa. A, Respiratory horn. B, Operculum. C, Caudal segment, male. D, Caudal segment, female, E, Dorsal tubercles. F, ad tubercle. G, dl tubercle. H, Abdominal chaetotaxy.

comb (Fig. 8D) with 5 spines, second from spur longest. Wing (Fig. 8E) uniformly grayish with pale spot on anterior margin just past second radial cell. Halter pale. *Abdomen:* Brown. Two slightly unequal spermathecae (Fig. 8F), plus rudimentary third; functional spermathecae with short slender necks; length 44 (35–51, n = 18) μ for larger, 42 (34–50, n = 17) μ for smaller.

Male: *Genitalia* (Figs. 8G–H): Sternite 9 with broad moderately deep caudomedian excavation, ventral membrane spiculate; tergite 9 with prominent triangular apicolateral processes, moderately broad, slightly divergent; the caudal margin between them transverse without medial cleft. Gonocoxite moderately stout; ventral root more slender than dorsal root; gonostylus curved distally, moderately slender, with moderately broad blunt tip. Aedeagus Y-shaped; basal arch extending half of total length; basal arms short, moderately slender, recurved at extreme apex, distal portion moderately broad. Paramere (Fig. 8H) with distinct anterior process; midpoint straight; apex diverging with three sharp medial spines, tip sharply pointed, diverging.

Distribution.—Mojave and Colorado deserts of southern California.

Material examined.—HOLOTYPE: ♀, Riverside County, CA, Deep Canyon, nr. Palm Desert, 29-VI-89 (B. A. Mullens), CO_2-baited trap. Allotype: ♂, San Bernardino County, CA, Big Morongo Canyon,

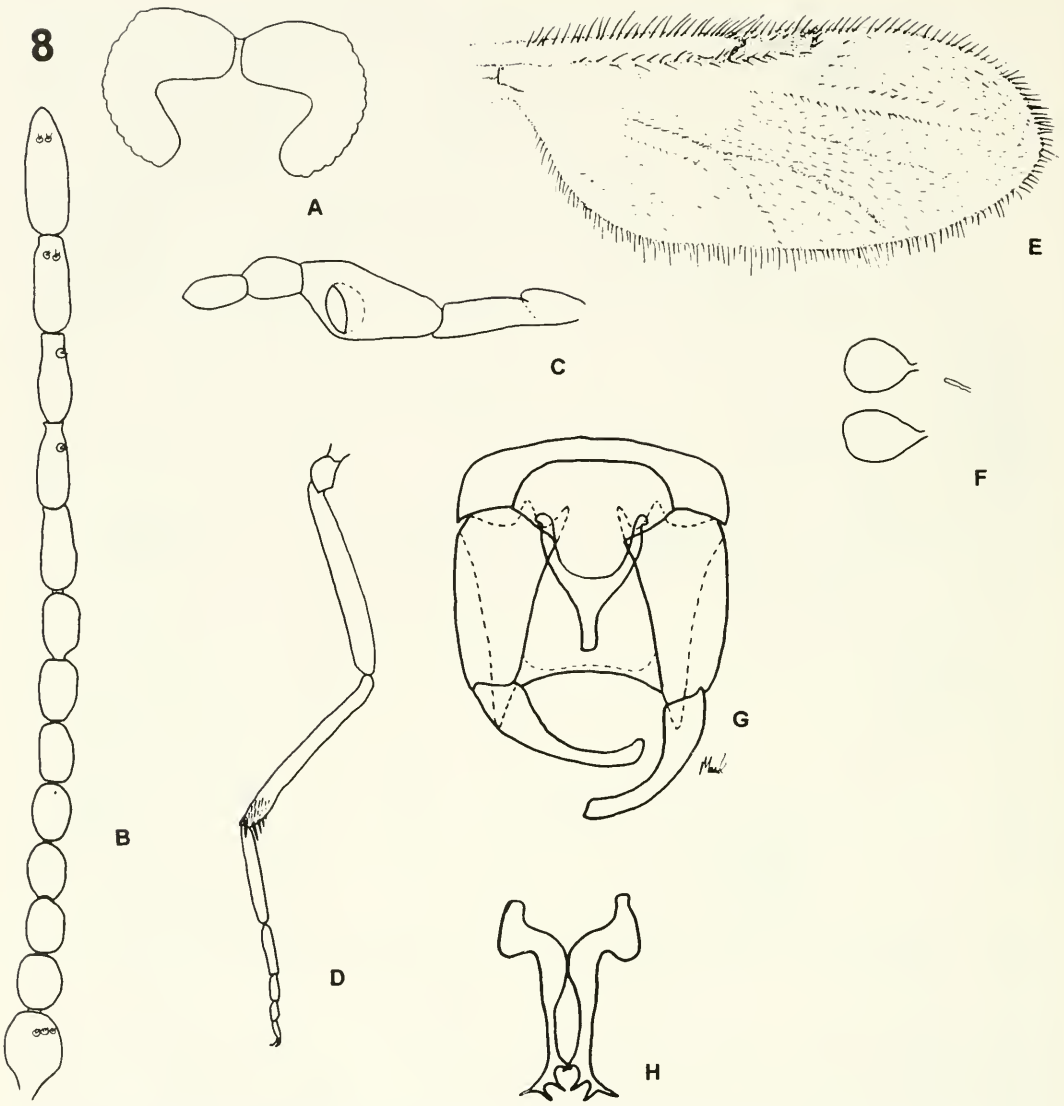

Fig. 8. *Culicoides vetustus*, adult. A–F, Female. G–H, Male. A, Eye separation. B, Antenna. C, Palpus. D, Hind leg. E, Wing. F, Spermathecae. G, Genitalia, parameres omitted. H, Parameres.

Morongo Valley, 15-VI-95 (Breidenbaugh), laboratory-reared from wild-collected female. PARATYPES: 1 ♀, same data as allotype; 16 ♀, 11 ♂ same data as allotype, except collected between 14-V-96 and 2-VII-96, some reared from wild-collected ♀; 9 ♀, San Diego County, CA, Anza Borrego State Park, Yaqui Well, 26-IV-97 (Breidenbaugh), CO_2-baited trap.

Biology and rearing.—Adult females collected in CO_2-baited traps readily fed through an artificial membrane and deposited eggs in the laboratory. Larvae exhibited the slowest development of any species reared on the agar system. Average clutch size was 86 ± 35 eggs (n = 52 females); these hatched in 7 ± 1 days with 67 ± 25% fertility (n = 25 females). Average development period to pupation was 117 ± 28 days (n = 46). Adults emerged 4 ± 1 days later (n = 39).

It is not known if the rearing medium

was responsible for the slow development or whether this is the normal condition for larvae of this species. The percentage of larvae reaching adulthood (approx. 31%) was similar to the other species reared (Breidenbaugh and Mullens, in preparation). Despite extensive observations, larvae were never seen feeding on nematodes; thus, this species was probably utilizing other microorganisms present in the cultures.

Discussion.—As discussed by Blanton and Wirth (1979), adults of a number of Nearctic *Culicoides* do not key readily to the subgenera described by Vargas (1960). This is true for *C. vetustus*. From adult and larval characteristics presented here, we are tentatively placing *C. vetustus* in the *biguttatus* species group. For example, the mandibles of the larvae resemble those illustrated by Murphree and Mullen (1991) of *Culicoides biguttatus* (Coquillett) and *Culicoides spinosus* Root and Hoffman except for the depth of the notch on the subapical margin of the mandible of *C. vetustus*. The number of dorsal-comb teeth (5) on the epipharynx is the same for *C. spinosus*. However, the lateral arms of the epipharynx are notched in *C. vetustus*, but not in *C. spinosus* or *C. biguttatus*. The hypostoma of *C. biguttatus* and *C. vetustus* are very similar.

The pupal operculum of *C. vetustus* resembles that of *C. biguttatus* and *C. spinosus*. However, the operculum of *C. vetustus* has fewer spines, and these are limited to the lateral margins. The respiratory horn of *C. vetustus* is more similar to that of *C. spinosus*, darkened at the tip and with 3 spiracular openings visible.

The range of *C. vetustus* overlaps only with *C. sublettei* Atchley and *C. usingeri* Wirth of the *biguttatus* group. The male genitalia of these species are similar in several respects, including the general shape of the parameres.

The apices of the parameres of *C. vetustus* are divided into 3–4 short spines and the distomedian process of the aedeagus is bluntly rounded. The aedeagus of *C. vetustus* is more slender than that of *C. sublettei* or *C. usingeri*, and there are 5 tibial spines in *C. vetustus* and *C. sublettei*, but 4 in *C. usingeri*. The females of *C. vetustus* lack a very distinctive wing pattern. However, they can be distinguished clearly from the other species in the *biguttatus* group and from *Culicoides piliferus* Root and Hoffman, which it superficially resembles, by the sensorial pattern (1, 11–13).

Etymology.—Latin *vetustus* for long-lived, referring to the lengthy development period of the larvae.

Discussion

Most descriptions of *Culicoides* species have included only the adult stage or in some cases, only the female. This is a result of the relative difficulty in locating developmental sites or collecting and associating males. The collection of host-seeking females, use of an artificial host, and a laboratory rearing system proved a very successful way of associating immature stages with adults. This approach should be useful for many species whose adults are known. The rearing technique is advantageous in that the entire cohort from an isofemale is unquestionably conspecific. In contrast, field-collected larvae, if they are located, generally must be killed and slide-mounted for identification. Consequently, an incorrect association with other larvae in the collection which have been reared to adults is possible.

The rearing method used here probably results in a narrower range of measurements for morphometric analysis, than if field-collected material were examined. Environmental homogeneity and the genetic similarity of laboratory-reared sibling larvae can result in morphological measurements that are unnaturally similar. The descriptions herein, however, will allow field-collected immatures to be identified and measured to better characterize the range of natural variability in characters such as size.

Acknowledgments

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BLASTOBASIS GRAMINEA, NEW SPECIES (LEPIDOPTERA: GELECHIOIDEA: COLEOPHORIDAE: BLASTOBASINAE), A STEM BORER OF SUGAR CANE IN COLOMBIA AND VENEZUELA

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Abstract.—***Blastobasis graminea*, new species**, a stem borer of sugar cane in Colombia and Venezuela, is described and illustrated. For the first time, a larva of Blastibasini is described in detail. Scanning electron micrographs of the larva, illustrations of the larval mandible, setal maps, and photographs of larval damage and pupation sites are provided. *Auximobasis obstricta* Meyrick 1918, is transferred to *Blastobasis* Zeller 1855, **n. comb.**, and *Blastobasis subolivacea* Walsingham 1897, is transferred to *Holcocera* Clemens 1863, **n. comb.**

Key Words: Coleophoridae, Blastobasinae, *Blastobasis*, sugar cane, Colombia, Venezuela

For decades, entomologists have known that larvae of at least one species of microlepidoptera other than *Diatraea saccharalis* (Fabricius) (Crambidae) feed on sugar cane and related grasses in Latin America. Although adult specimens of one species of Coleophoridae (Blastobasinae) have been collected since the late 1940's and 1950's by H. E. Box in Venezuela and during the early 1970's and 1980's by L. Cárdenas and others in Colombia, this moth remained nameless.

Because many Blastobasinae are similar in wing pattern, they are frequently misidentified. For example, the species described herein, *Blastobasis graminea*, had been previously misidentified as *Auximobasis obstricta* Meyrick 1918, (Box 1953, Guagliumi 1962) and *Blastobasis subolivacea* Walsingham 1897, (Martorell 1976). In addition, type specimens of Neotropical Blastobasinae have not been studied systematically until recently.

Since Meyrick (1894) the Blastobasinae have long been considered to be monophyletic; recent studies (Adamski and Brown 1989, Hodges, in press) have corroborated this notion and postulated phylogenetic relationships of the Blastobasinae within Gelechioidea. In this study, the Blastobasidae (*sensu* Adamski and Brown 1989) are treated as a subfamily within the Coleophoridae, following Hodges (in press).

The purpose of this paper is to describe and illustrate *Blastobasis graminea*, new species, and to make available to entomologists and sugar cane growers a means by which to identify it.

Adult and larvae were examined using an incandescent light source (reflected light). Kornerup and Wanscher (1978) was used as a color standard for the description of the adult. Genitalia were dissected as described by Clarke (1941), except Mercurochrome and chlorazol black were used as stains. Slide preparations were examined with dissecting and compound microscopes. Measurements were made with a calibrated ocular micrometer. All specimens examined are deposited in The National Museum of

Fig. 1. Holotype of *Blastobasis graminea*.

Natural History, Smithsonian Institution, Washington, D.C., (USNM), except where indicated otherwise. Label data taken verbatim are expressed with quotations, while bracketed data are used to complete label data written in abbreviated form, or to help with the recognition of certain labels by description of condition, e.g., [round label].

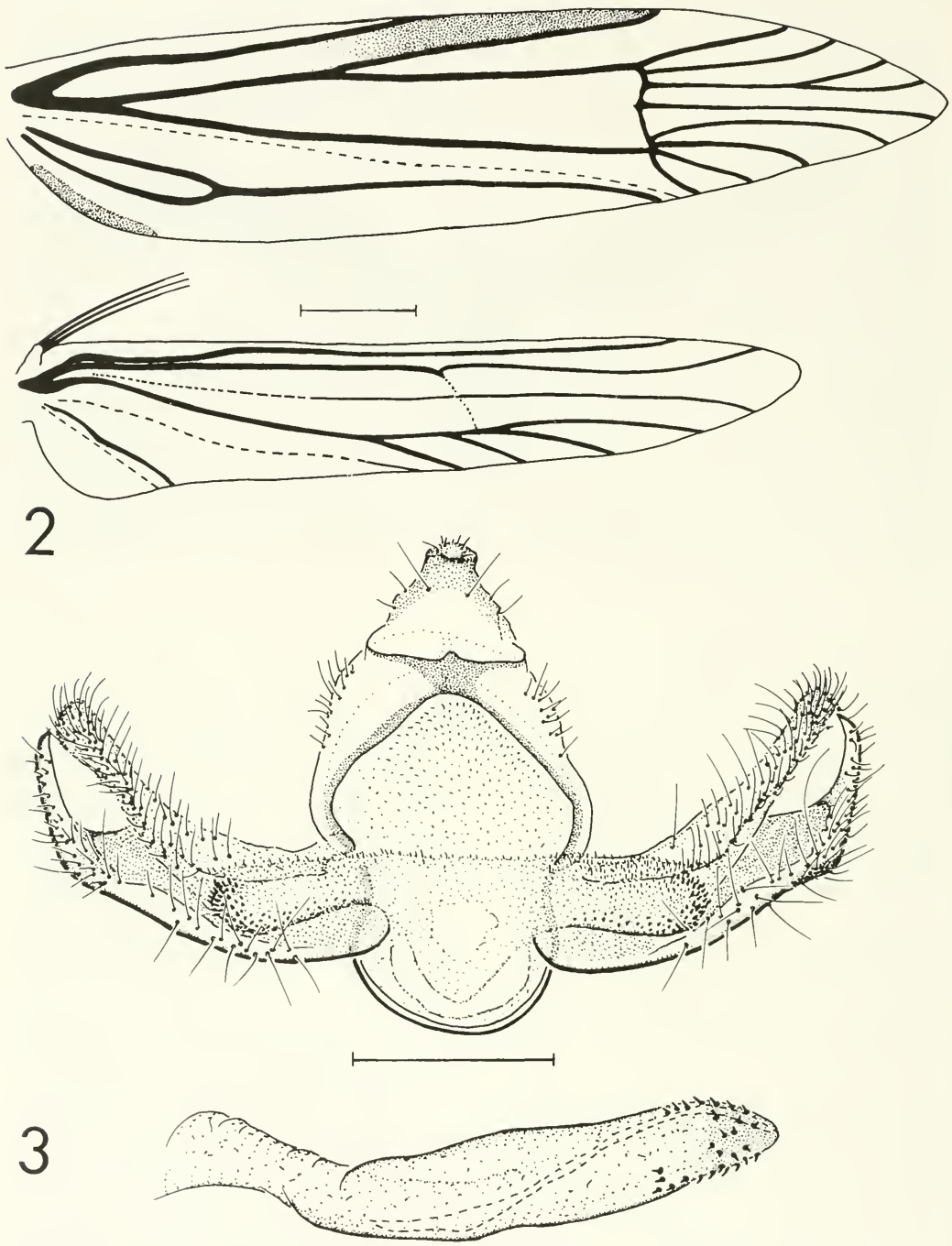
The ultrastructure of the larva was studied with an Hitachi HH-S-2R scanning electron microscope at an accelerating voltage of 20 kV. For SEM examination, larvae were fixed in 3% glutaraldehyde in 0.1 M potassium phosphate buffer (pH 7.3), rinsed in phosphate (pH 7.3), and postfixed in 2% osmium tetroxide in 0.1 M potassium phosphate (pH 7.3). After dehydration in ethyl alcohol, specimens were critical point dried, mounted on stubs with silver paint and paste, and coated with gold-palladium in a Polaron E5100 sputter coater.

Blastobasis graminea Adamski, new species
(Figs. 1–26)

Diagnosis.—*Blastobasis graminea* can be distinguished from other *Blastobasis* by the orange gray ground color, wide base of the uncus, rounded outer margin of the proximal flange, and wide ostial opening.

Adult.—*Head:* Cephalic vestiture pale orange gray, except inner surface of labial palpus pale orange gray intermixed with brown scales tipped with white and few dark-brown scales, outer surface mostly brown intermixed with brown scales tipped with white, pale orange-gray scales, and dark-brown scales; segments paler near apical region.

Thorax: Tegula and mesoscutum pale orange gray; legs with outer surface pale orange gray intermixed with orange-gray scales tipped with white, most specimens with foreleg and midleg with outer surface mostly grayish brown intermixed with grayish-brown scales tipped with white, orange-scales, and orange-gray scales tipped with white, leg segments and tarsomeres paler near apical region; forewing (Fig. 1), length 7.1–10.0 mm [n = 37], orange gray intermixed with orange gray scales tipped with white, brown scales tipped with white, and brown scales; several unrubbed specimens with discal cell region paler than out-



Figs. 2, 3. *Blastobasis graminea*. 2, Wings, scale = 1.00 mm. 3, Male genitalia, scale = 0.5 mm.

er region of wing; holotype with a brown streak on basal part of posterior margin (Fig. 1); some specimens with veins demarcated with white scales; a dark brown midcell spot and two distal spots usually present; fringe scales mostly orange gray tipped with white intermixed with orange gray scales; undersurface grayish brown;

cubitus four-branched, divergent from radials and M_1 (Fig. 2); hindwing with both surfaces pale grayish brown; cubitus four-branched in a series typical of all New World *Blastobasis* (Fig. 2).

Abdomen: Orange gray.

Male Genitalia (Fig. 3): Uncus wide at base, posteriorly curved and narrowed apically, apical setae shorter than basal setae; gnathos bidentate; dorsal strut narrow; tergal setae numerous; diaphragma with microtrichia throughout, extending to proximal flange; proximal flange with stout marginal setae, margin rounded; lower part of valva with marginal setae, numerous along apical third; juxta bandlike; aedoeagus apically rounded, with several stout anellar setae.

Female Genitalia (Fig. 4): Ovipositor telescopic, in four membranous divisions; ostium within membranous area slightly posterior to seventh sternum; ostial opening wide; antrum membranous, narrowed abruptly anteriorly forming a common inception for ductus seminalis and ductus bursae; ductus bursae long, with two rows of platelike sclerotizations within anterior part; corpus bursae with posterior lobe near inception of ductus bursae; signum hornlike.

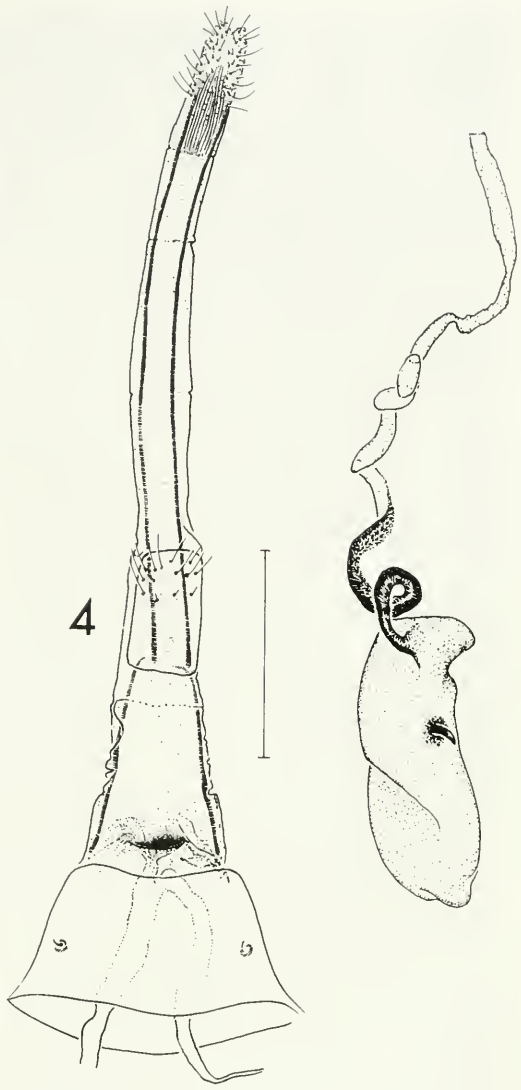
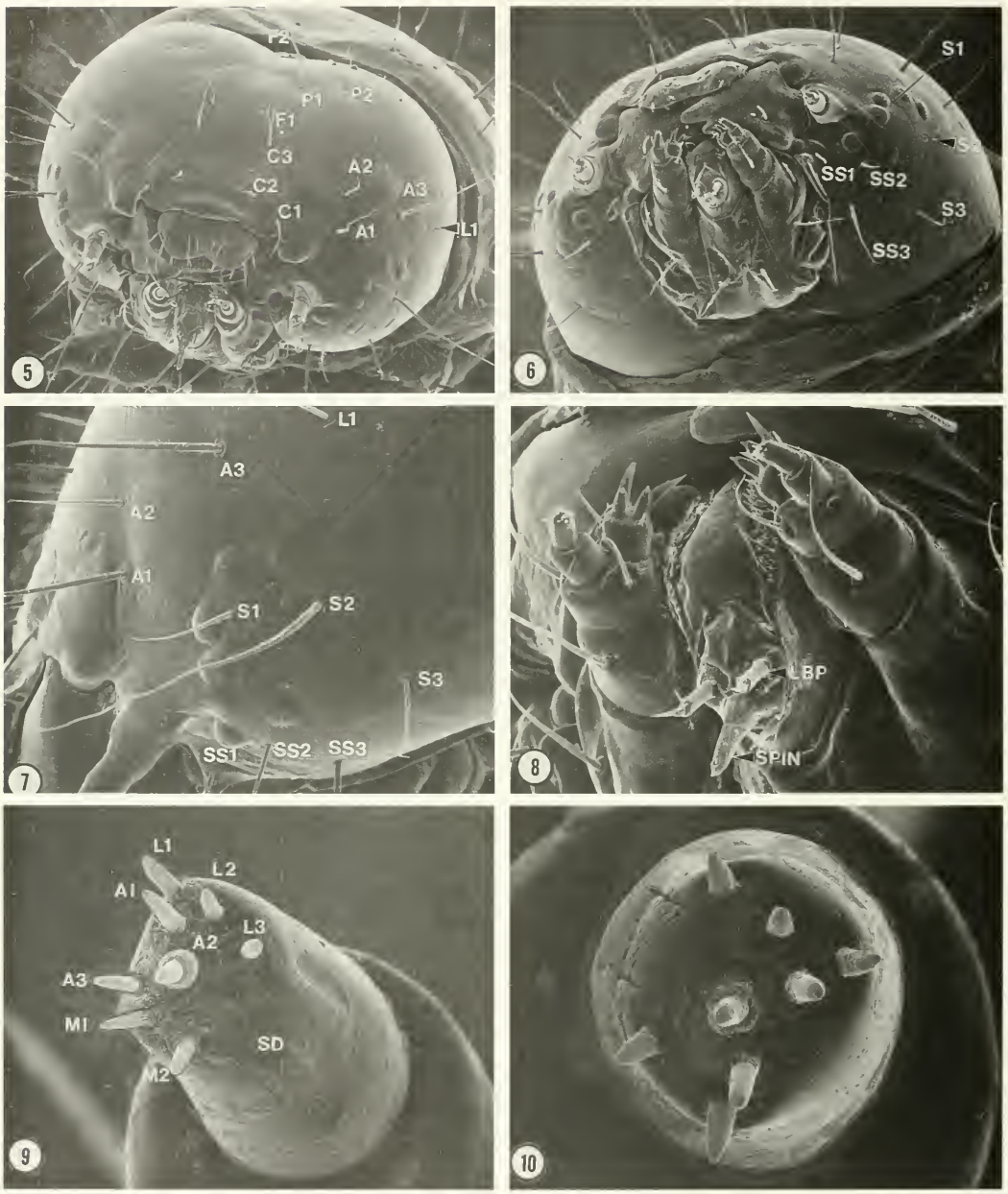


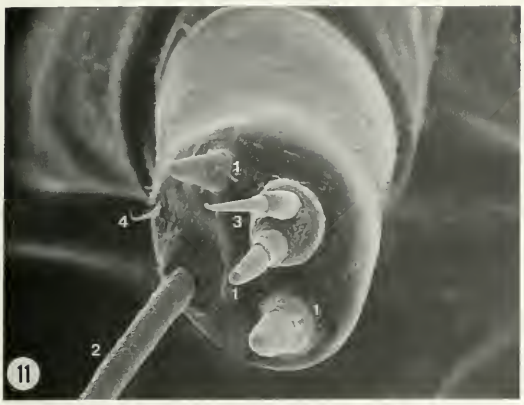
Fig. 4. Female genitalia of *Blastobasis graminea*. Scale = 1.00 mm.

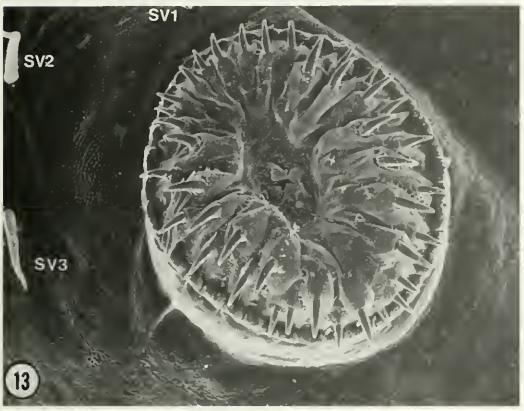
Larva.—Length 6.5–14.9 mm [n = 207]. Body white, smooth, with head capsule, prothoracic shield, anal shield, pinacula and crochets yellowish orange. *Head* (Figs. 5–12, 17, 18): Hypognathous; epicranium smooth; adfrontal sclerites narrow, delimiting frons dorsolaterally; frons closed; C1, C2, and C3 about equal in length, about three times length of F1 and F2; C3 closer to F1 than to C2; C2 slightly closer to midline than C1 or C3; C1 setae broadly curved, convergent; F1 subapical (Fig. 5); P1 long, closer to P2 than A2; A2 closer to A1 than A3; A3 nearly equidistant to A2 and L1 (Figs. 5–7); S1 between stemmata 2 and 3, and closer to S2 than to S3; SS1 near mandibular articulation, and closer to SS2 than to SS3; SS2 between stemmata 5 and 6 (Figs. 6, 7); labrum bilobed, each lobe with four subequal marginal setae and two subequal medial setae (Figs. 5, 6); mandibles slightly asymmetrical, with two distinct dentitions and two subequal setae on outer margin (Figs. 5, 6, 17); labium smooth with microtrichia along lateral margin of proximal half; distal part of labium with median submental pit (Figs. 6, 8); labial palpus two-segmented, with dorsally directed subapical seta on basal segment. Sensilla types and arrangement on median

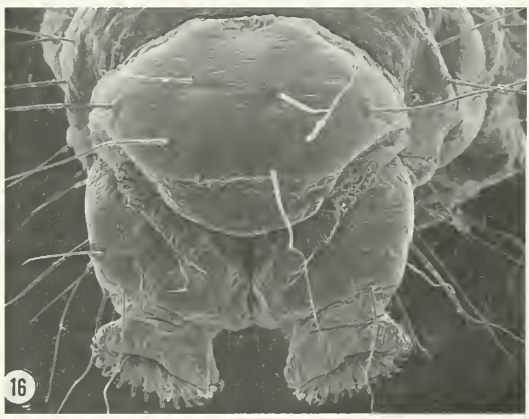


Figs. 5–10. SEM of larva of *Blastobasis graminea*. 5, Frontal view of head capsule, 70×. 6, Ventral view of head capsule, 70×. 7, Lateral view of genal region of head capsule, 250×. 8, Ventral view of labium, LBP = labial palpus, SPIN = spinneret, 250×. 9, 10, Sensilla on apex of maxillary palpus, A2 = sensillum styloconicum; A1, M1, M2, L1, L2, L3, = sensilla basiconica; SD = sensilla digitiform, 2,500×.

lobe and apex of palpus similar to that of *Glyphidocera juniperella* Adamski and Brown 1987, except for elongate depression near digitiform sensillum on part near L3 sensillum (Figs. 8–10). Sensilla types on antenna (Fig. 11) similar to other Lepidoptera (Schoonhoven and Dethier, 1966). *Prothorax* (Figs. 12, 18): Prothoracic shield with SD1 and D2 about equal in length, twice length of XD1 and XD2; SD1 and D2

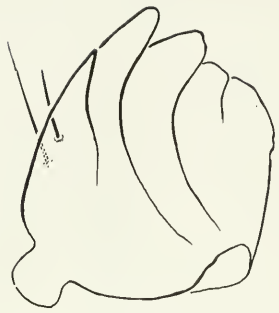






Figs. 11–16. SEM of larva of *Blastobasis graminea*. 11, Sensilla on apical portion of antenna. 1 = sensilla basiconica; 2 = sensillum chaetica; 3 = sensullum styloconicum; 4 = sensillum trichodeum, 950×. 12, Lateral view of head capsule and thorax, 45×. 13, Ventral view of right proleg on A4, 200×. 14, A8-10, 60×. 15, Lateral view of A10, 80×. 16, Posetrior view of A10, 80×.

about four times length of SD2 and D1; D1 usually slightly longer than SD2; SD2 closer to SD1 than to XD2; SD2 and D2 anteriorad to D1; L1 about twice length of L2 and L3; SV1 about twice length of SV2; V1 short (not illustrated). *Mesothorax and metathorax* (Figs. 12, 18): D1 anterodorsal to D2, on same pinaculum; D2 about three times length of D1; SD1 anterioventral to SD2, on same pinaculum; SD1 about three



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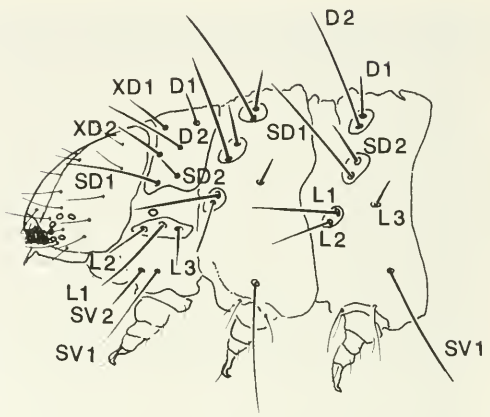

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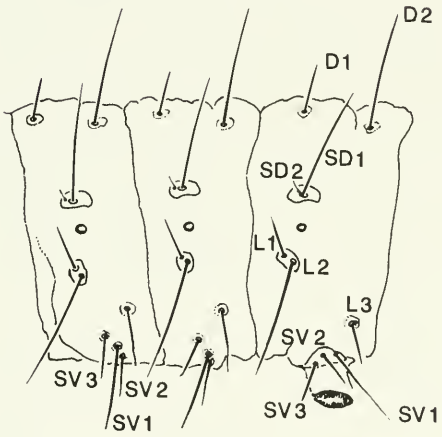

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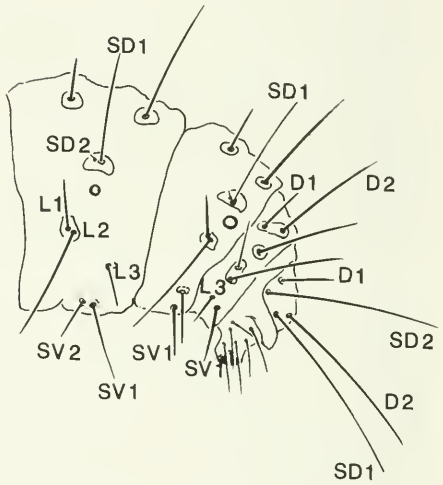

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Figs. 17–20. Larva of *Blastobasis graminea*. 17, Left mandible. 18, Lateral view of head capsule and thorax. 19, A1-3. 20, A7-10.

times length of SD2; L2 anterioventral to L1, on same pinaculum; L1 slightly longer than L2 and about three times length of L3; SV1 about equal in length to L1 and slightly caudal to L3; V1 short (not illustrated). *Abdomen* (Figs. 13–16, 19, 20): A1 and A2 with D2 three times length of D1; SD1 about same length as D2; SD2 very short (Figured larger than normal), on same pinaculum as SD1 above spiracle; L1 anterodorsal to L2, L2 about twice length of L1; L3 caudal to D2, about equal in length to L1; SV3 2–3 times length of SV2 and SV1; SV2 and SV1 in nearly straight line perpendicular to longitudinal body axis, SV3 slightly anterior to SV1; V1 short (not illustrated); A3–A6 with SV1 posterior to SV2; prolegs with crochets uniserial and triordinal, crochets smaller along outer margin of planta; A7 with SV3 absent; A8 with SD1 hairlike; one SV seta present; SV1 nearly in verticle line with L3 and V1; SV1 and L3 about equal in length, V1 short (not illustrated); spiracle slightly larger than prothoracic and other abdominal spiracles; A9 with SD2 absent; L3 ventral to L2; SV1

caudal to D2; V1 short (not illustrated); A10 (Figs. 14–16, 20): D2, SD1, and SD2 about four times length of D1; crochets uniserial and triordinal.

Holotype.—♀, "Colombia: Instituto Colombiano Agropecuario, Experiment Station "Palmira," Cauca Valley, 1 March–15 March 1991, Ex. Sugar cane, Coll. Lucero Cárdenas Duque, Emerged 21 April–1 May 1991." The holotype is not dissected and is deposited in USNM.

Paratypes.—3 ♀, Same data as holotype. Paratypes are not dissected and are deposited in USNM.

Other specimens examined.—COLOMBIA: 2 ♂, 7 ♀, "Miranda (Val.), en. caña a [zúcar], Jul[y] 1984, L[ucero] Cárdenas"; 1 ♂, 1 ♀ from Vitor Becker Collection [yellow label]; 1 ♂, 5 ♀, "Miranda, VI-28–[19]84, L[ucero] Cárdenas," "Tallos caña de azúcar," "♀ Wing Slide by DA 3349, USNM 81585," [green label]," "♀ Genitalia Slide by D. Adamski 2885, USNM 81422," [green label]; 3 ♀, "Riopaila, Parasita *Diatraea*," "I-6–[19]65, 723–4," "II-1–[19]65, 9651–28," "II-15[19]65, 446–1"; 1 ♂, 1 ♀, "Ex. sugar cane, Ag. Exp. Sta., Palmira, Valle, Let. Oct. 3, 1941, B. Losada S," "♀ Genitalia Slide by R. B. Selander, USNM 11, 157," [green label]; 2 ♀, "Valle Ingenio del Cauca, H: caña de azúcar, Barrenador, Dic/[19]82, D-83," "♀ Genitalia Slide by D. Adamski 2849, USNM 81393," [green label], "♀ Genitalia Slide by D. Adamski 2850, USNM 81394," [green label]; 2 ♂, 1 ♀, "Valle Ing[enio] del Cauca, H: caña de azúcar Col: L[ucero] Cárdenas y Y.P. Chacon, II-[19]83, D-83," "♂ Genitalia Slide by D. Adamski 2847, USNM 81391," [green label], "♂ Genitalia Slide by D. Adamski 2846, USNM 81390," [green label], "♀ Genitalia Slide by D. Adamski 2848, USNM 81392," [green label]. VENEZUELA: 2 ♀, "Tachira, El Cobre, 12,00 m[e]t[e]rs, May 1947," and "Tachira, La Grita, 1,450 m[e]t[e]rs, 14.V.1949," "Reared from larva in Sugar cane," "♀ Genitalia Slide by R. B. Selander, USNM 11160," [green label], "♀ Genitalia Slide by R. B. Selander, USNM 11161" [green label]; 2 ♂, 1 ♀, "Maracay, 450 m[e]t[e]rs, 28.iii.1949, H.E. Box", "February 1951," "June 1948," "Reared from larva in Sugar cane," "♂ Genitalia Slide by D. Adamski 3038, USNM 81488" [green label], "♂ Wing Slide by J. G. Clarke, USNM 11209" [green label], "♂ Genitalia Slide by J. G. Clarke, USNM 11209" [green label], "♀ Genitalia Slide by R. B. Selander, USNM 11164" [green label]; 1 ♀, "Carabobo, Cent. Tacarigua, 450 m[e]t[e]rs, September 1947, H.E. Box," "Reared from larva in Sugar cane," "♀ Genitalia Slide by R. B. Selander, USNM 11159" [green label], 1 ♂, 3 ♀, "Yaracuy, Chivacoa, 230 m[e]t[e]rs, February 1950," "28.ii.1950," "San Pa[illegible], 400 m[e]t[e]rs, 22.ii.1949, H.E. Box," "Reared from larva in Sugar cane," "♂ Genitalia Slide by D. Adamski 3037, USNM 81487," [green label], "♀ Genitalia Slide by R. B. Selander, USNM 11163" [green label], "Reared from larva in Sugar cane," "♀ Genitalia Slide by J. G. Clarke, USNM 11210" [green label], "Reared from larva in Sugar cane," "♀ Genitalia Slide by R. B. Selander, USNM 11162," [green label], "Reared from larva in Sugar cane"; 1 ♂, "Merida, nr. Egido, 1,500 m[e]t[e]rs, 8.VI.1949, H. E. Box," "♂ Genitalia Slide by D. Adamski 3039, USNM 81489" [green label]; 1 ♀, "Miranda, Sta. Lucia, 180 m[e]t[e]rs, 5.iii.1948, H.E. Box," "♀ Genitalia Slide by J. C. Clarke, USNM 11207" [green label], "Reared from larva in Sugar cane"; 1 ♀, "Aragua, El Conseja, 550 m[e]t[e]rs, March 1951, H.E. Box," "Reared from larva in Sugar cane," "♀ Genitalia Slide by R. B. Selander, USNM 11158" [green label]; 1 ♂, "El Limon, nr, Maracay, 460 m[e]t[e]rs, 31.iii.1950, H.E. Box," "Reared from larva in *Ciox lachryma-jobi* [L]"; 1 ♀, "Zulia, Perijo, Mts. close to Colombia, Dec. 1950, F. Fernandez Yepoz," "Reared from larva in *Setaria paniculifera* [Fournier]," "♀ Genitalia Slide by J. F. Clarke, USNM 11208" [green label]; 1 ♀, "Vene-

zuela, Turbio Valley, nr. Barquisimeto, 1956, P. Guagliumi, Larva boring sugarcane, COM. INST. ENT. COLL. NO. 15211, Press[ented] by Com. Inst. Ent., BM 1957-256." Fourteen additional adult specimens were examined at The Natural History Museum, London, with above label data. Larvae studied were collected and preserved in alcohol with the following data, "Colombia: Instituto Colombiano Agropecuario, Experiment Station "Palmira," Cauca Valley, 15 December–20 January 1990, Ex. Sugar cane, Coll. Lucero Cárdenas Duque." All larval specimens are deposited in the USNM alcohol collection.

Types examined.—Lectotype designated by Clarke, ♂, *Blastobasis obstricta* Meyrick, "Lectotype" [round label], "Bartica, Brit[ish] Guiana, Parish 1.13," "Lectotype, *Auximobasis obstricta* Meyrick, J.F.C.C. 1948," "♂ Genitalia on Slide 5-X-1948, J.F.G.C. 8078," *Auximobasis obstricta* Meyr., E. Meyrick det., in Meyrick Coll. 21/1," "*obstricta* Meyr.," "Meyrick Coll., BM 1938-290," [Natural History Museum, London, England]. Lectotype, ♂, *Blastobasis subolivacea* Walsingham, "S[aint] Thomas, 9.IV.[18]94" [hand-written pink label], "*Blastobasis subolivacea* 125.2089 WLSM, ♂, TYPE" [hand-written label], "♂ Genitalia Slide by D. Adamski, 3470" [green label], "Holotype, *Blastobasis subolivacea* Wlsm, ♂," ["Grigore Antipa" National Museum of Natural History, Bucharest, Romania].

Etomology.—*Blastobasis graminea* is named after the plant family Gramineae because larvae feed on several grass hosts.

Discussion

Auximobasis obstricta Meyrick 1918, is transferred to *Blastobasis* Zeller, 1855, and *Blastobasis subolivacea* Walsingham, 1897, is transferred to *Holcocera* Clemens 1863 (**new combinations**).

Blastobasis graminea is probably more closely related to *Blastobasis obstricta* Meyrick, 1918, n. comb. than to any other described *Blastobasis*. Both species differ markedly in wing pattern and in several male and female genitalic features. However, males of both species share an uncus with a widened base, a bidentate gnathos, and stout marginal setae along the outer margin of the proximal flange. Females share a widened ostium.

Martorell (1976) reported two species of Blastobasidae feeding within sorghum heads in the Vieques Islands east of Puerto Rico, but I have not seen any specimens to substantiate this.

Biology

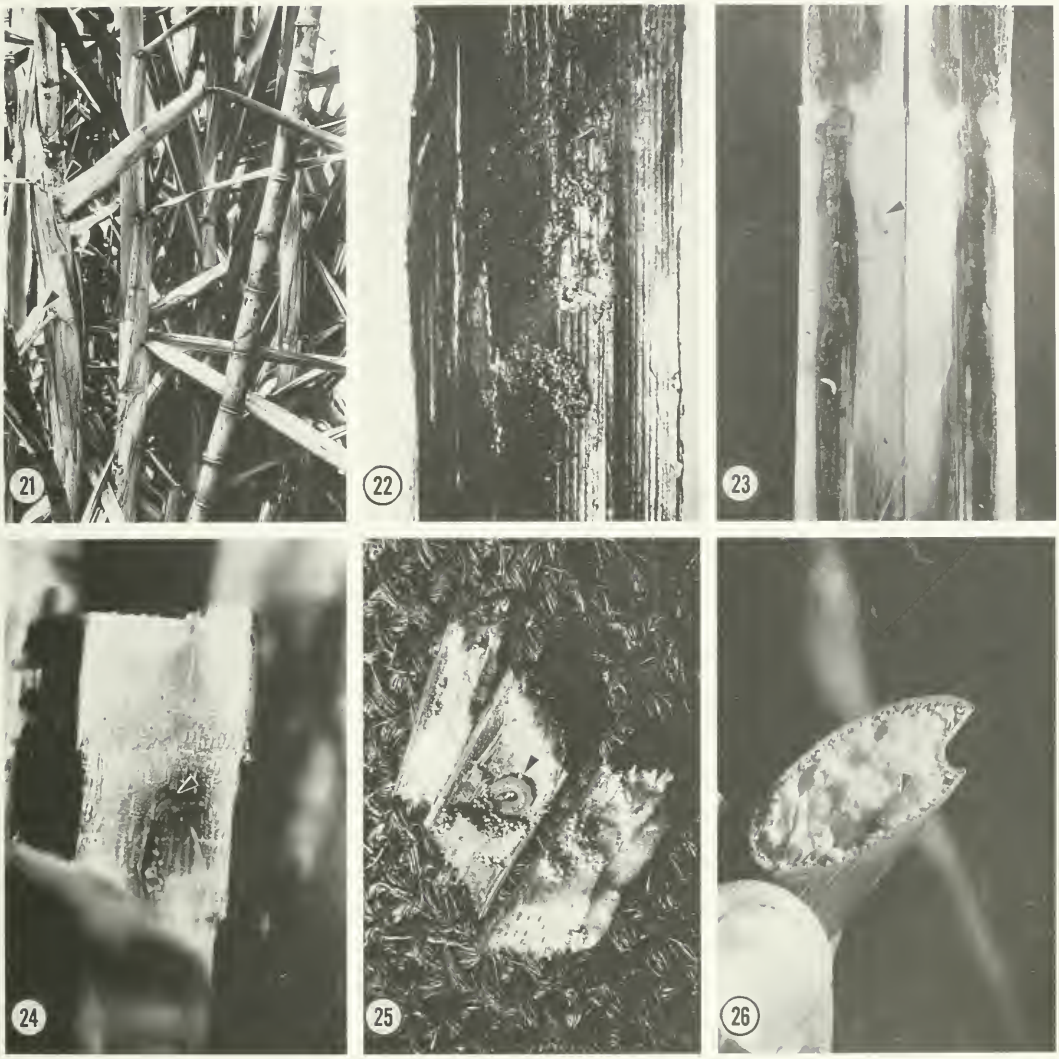
Cárdenas and Hernández (1985) described the biology of *Blastobasis graminea* on sugar cane in Colombia; these findings are summarized below. The most severe damage by *B. graminea* occurs within the terminal third of the sugar cane plant, however, damage can occur in lower regions as well. When the damage is extreme the apical portion of the plant dies.

Early instars of *B. graminea* feed on the surface tissue layers. When the larva is able, it bores into the stem. Galleries are usually irregularly shaped (Figs. 22–24); the larvae never excavate more than two internodes of the plant. Mature larvae usually pupate between the stem and the sheath (Fig. 21), but sometimes within the stem (Fig. 22). In addition to sugar cane, larvae feed on corn (Figs. 25, 26), sorghum, *Coix lacryma-jobi* L., and *Setaria paniculifera* Fournier.

There appears to be a strong correlation (Ratio of 8:1) between the presence of *Diatraea saccharalis* and *Blastobasis graminea*, however, it is not known which moth species attacks the plant first.

Acknowledgments

I thank Ingeborg Zenner-Polania, former director, Programa de Entomología, Instituto Colombiano Agropècuario, Bogotá, Colombia, for the coordination of activities related to the acquisition of specimens of *Blastobasis graminea*; Lucero Cárdenas Duque, of the above institution, for live and



Figs. 21–26. Larval damage of *Blastobasis graminea*. 21, Pupal site on sugar cane (see arrow). 22, Pupa within sheath of sugar cane (see arrow). 23, Larvae and damage within sugar cane stem (see arrow). 24, Larval gallery within sugar cane stem (see arrow). 25, Larval damage in corn stem (see arrow). 26, Larva within corn stem (see arrow).

preserved larvae, and photographic prints of larval damage; Klaus Sattler, Michael Shaffer and Kevin Tuck, of the Natural History Museum, London, England, for their help with examination and photography of type specimens; Dorel Rusti, "Grigore Antipa" National Museum of Natural History, Bucharest, Romania, for the loan of the lectotype of *Blastobasis subolivacea* Walsingham; Greta Tyson and Michael Sullivan, of the Electron Microscope Center, Mississippi State University, for their help with the preparation of the specimens and photographic plates; Carl Hansen of the Office of Imaging, Printing and Photographic Services for the photograph of the holotype; the late John F. Gates Clarke, Smithsonian Institution, for referring this research problem to me. This research was supported in part by NSF Grant BSR85-01212 and a grant from Sigma Xi.

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A REVISION OF THE *FLAVIDUS* GROUP OF THE GENUS *CHRYSOPS* MEIGEN (DIPTERA: TABANIDAE)

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Abstract.—A taxonomic revision of the *Chrysops flavidus* species group is provided with a key to species, descriptions, distribution maps, and illustrations of wings and antennae for each of the nine species currently recognized in this group. The relationships and identification of these nine species are based on analysis of morphological similarity involving 13 critical characters. A total of 4,843 specimens from 14 institutions were examined during this study. Two new species in the *Chrysops flavidus* group are described, ***Chrysops sandyi*** and ***Chrysops tumidicornis,*** both previously misidentified as *Chrysops atlanticus.* The male of *Chrysops dixianus* is described for the first time.

Key Words: Diptera, Tabanidae, *Chrysops flavidus* group, key to species

The genus *Chrysops* Meigen is currently represented by 87 described species in the Nearctic Region north of Mexico (Burger 1995), and 291 world wide. This genus was last revised in North America by Philip (1955). Philip's revision included a key to 95 species and 14 subspecies, with corresponding notes on these taxa, and descriptions of 4 new species and 5 new subspecies (but it also treated species from Central America and the Caribbean).

Although no one has divided all of the Nearctic *Chrysops* into definitive species groups, some species groups have been recognized by tabanid taxonomists. The three commonly used are the *Chrysops callidus* group, the *C. carbonarius* group, and the *C. flavidus* group (Pechuman 1949). The *C. flavidus* group is particularly difficult because of the large amount of intraspecific variation within the included taxa. Although three species have been described in this group during the past 45 years, no one has studied the group as a whole.

The *Chrysops flavidus* group currently includes 7 previoously described species and two new species: *Chrysops atlanticus* Pechuman, *C. brunneus* Hine, *C. celatus* Pechuman, *C. dixianus* Pechuman, *C. flavidus* Wiedemann, *C. pudicus* Osten Sacken, and *C. reicherti* Fairchild, *C. sandyi,* n.sp., and *C. tumidicornis,* n. sp. I will redescribe, clarify relationships and summarize the biology and geographic distribution of this group. Immature stages and habitat are discussed under the description of each species.

MATERIALS AND METHODS

I examined 4,843 specimens, (4,684 females and 159 males), from the collections listed below. The acronyms are those of Arnett et al. (1993), except for the University of New Hampshire Collection (UNHC).

AMNH: Department of Entomology, American Museum of Natural History, New York, NY; David A. Grimaldi.

BMNH: Department of Entomology, The

Natural History Museum, London, U. K.; John E. Chainey.

CASC: Department of Entomology, California Academy of Sciences, San Francisco; Paul H. Arnaud, Jr.

CNCI: Canadian National Collection, Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, Ontario; J. M. Cumming.

CUCC: Department of Entomology, Clemson University, Clemson, SC; Michael A. Floyd.

CUIC: Department of Entomology, Cornell University, Ithaca, NY; E. Richard Hoebeke.

FMNH: Division of Insects, Field Museum of Natural History, Chicago, IL; Alfred F. Newton, Jr.

FSCA: Florida State Collection of Arthropods, Division of Plant Industry, Gainesville; G. B. Fairchild.

INHS: Illinois Natural History Survey Insect Collection, Champaign; Kathleen R. Methven.

OSUC: Ohio State University, Collection of Insects and Spiders, Columbus; Andrey Sharkov.

TAMU: Department of Entomology Insect Collection, Texas A. & M. University, College Station; Edward G. Riley.

UGCA: Entomology Collection, University of Georgia, Athens; Cecil L. Smith.

UNHC: Entomological Museum, Department of Zoology, University of New Hampshire, Durham; Donald S. Chandler.

USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; R. V. Peterson.

The following insect collections are also cited in this paper:

MNHN: National Collection of Insects, Muséum National d'Histoire Naturelle, 45, Rue Buffon, Paris 75005 France.

MRSN: Museo Regionale Scienze Naturali, Via Gioletti 36, Torino 10128, Italy.

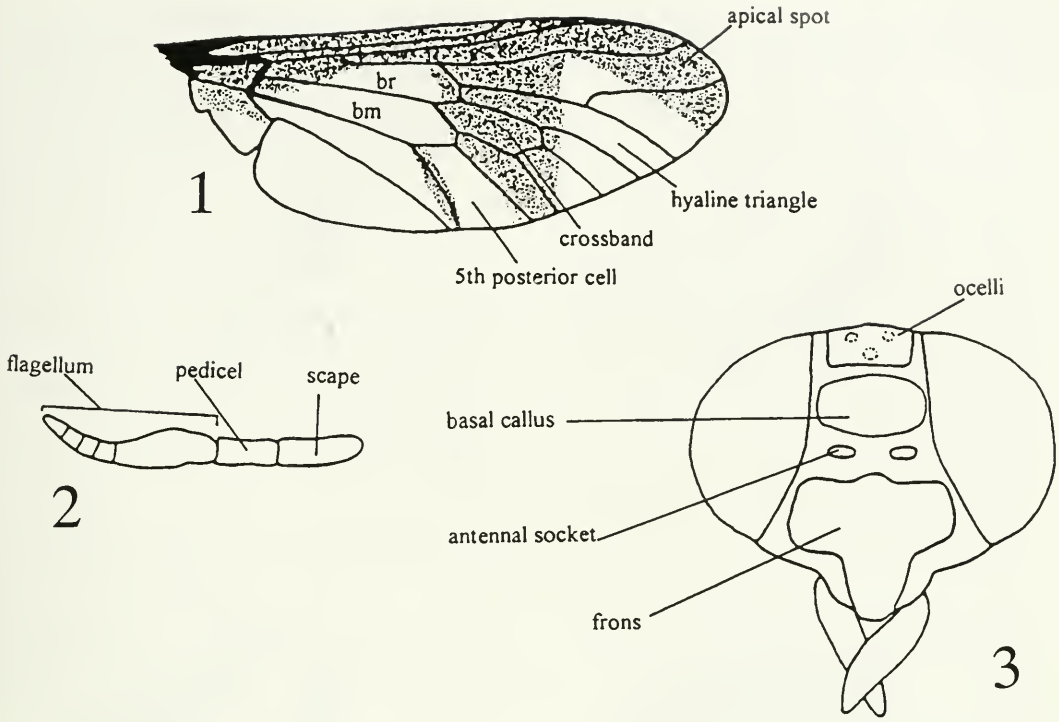
MZLU: Museum of Zoology, Lund University, Helgonavägen 3, S-223 62 Lund, Sweden.

ZMHB: Museum für Naturkunde der Humboldt Universität zu Berlin, Bereich Zoologischer Museum, Invalidenstraße 43, 1040 Berlin, Germany.

The *Chrysops flavidus* group has few distinctive structural characters, and the species can be difficult to identify. Color patterns are important in identification but must be used with caution because of variation. The characters described below are the most useful in separating the species. The morphological terminology used in this paper follows that used by Teskey (1990). Principal characteristics used are: body length, in millimeters, from the base of the antennae to the apex of the abdomen; the size and shape of the scape and pedicel as well as the length ratio and color of the scape, pedicel, and flagellum; shape of the frontal callus; color of the mesoscutum; wing pattern, particularly the width of the apical spot, the location of the outer margin of the crossband, and the infuscation of the 5th posterior cell; color of the hind femur; and abdominal color pattern.

For illustrations, I chose a specimen that most closely resembled the description of the holotype. One wing from each specimen was removed, placed between two 2 × 2 glass slides and scanned into a Dell 486p/25 computer using MICROTEK ScanMaker 35t. The scanned picture was printed and used as a template for the final drawing. The antennal drawings were produced with a camera lucida.

The locality data from all specimens examined were entered into a database using Wordtech Systems, dB*XL*®, (a dBASE III Plus® compatible format). The information collected was placed into 9 "fields": species, country, state, county, town, collector,



Figs. 1–3. 1, Wing of *Chrysops* species. 2, Antenna of *Chrysops* species. 3, Anterior view of head of *Chrysops* species.

museum, count (number of specimens with identical data), and sex (male or female). Locality data for specimens I did not examine were taken from the distribution records of L. L. Pechuman, now stored in the Zoology Department at the University of New Hampshire. Distribution maps were then produced for each species from the above database and from the records of L. L. Pechuman.

Diagnosis of the *Chrysops flavidus* Group

Frontoclypeus glossy yellow with no mid-facial stripe; frontal callus yellow to light brown, occasionally with brown upper margin; frons yellow pollinose; mesoscutum with 3 longitudinal stripes, darker than ground color; proepimeron and proepisternal callosity yellow tomentose with long yellow hair; wing pattern with broad apical spot entering 2nd submarginal cell, crossband reaching hind margin of wing, hyaline triangle not crossing vein R_{2+3}, cell br at least ⅓ infuscated basally; abdominal tergites 2–4 patterned with median inverted "V" set over pale median triangle.

Key to Species of the *Chrysops flavidus* Group

1. Scape and pedicel distinctly swollen, together longer than flagellum (Fig. 14). Frontal callus twice as wide as high, with no black markings. Abdomen with inconspicuous median triangles. Wing pattern with extensive apical spot, reaching crossband posteriorly and enclosing hyaline crescent (Fig. 23) . . . . . *brunneus* Hine
– Scape and pedicel less swollen, combined length equal to or shorter than flagellum. Without remaining combination of characters 2
2. Usual hyaline areas of wing slightly smoky to very smoky, outer margin of crossband angled from vein R_4 to middle of vein M_3 (Fig. 22). Scape and pedicel moderately swollen, combined length equal to or rarely longer than flagellum (Fig. 13). Mesoscutum green-gray iridescent with black longitudinal stripes . . . . . *atlanticus* Pechuman
– Without above combination of characters . . . 3

3. Mesoscutum greenish gray or steel gray in ground color, longitudinal stripes black. Outer margin of crossband sinuous 4
– Mesoscutum yellow in ground color, longitudinal stripes brown. Outer margin of crossband, straight, concave, or sinuous 6
4. Antenna not swollen, flagellum at least ⅓ longer than scape and pedicel combined (Fig. 15). Frontal callus spade shaped, width and height subequal. Without dark spot under scutellum . . . . . *celatus* Pechuman
– Scape and pedicel slightly swollen to swollen, combined length subequal to flagellum. Frontal callus, width and height not equal. Abdomen with dark spot under scutellum, often extending to lateral edges of tergite 1 5
5. Hyaline triangle not reaching vein R_{2+3}, cells br and bm ¾ and ⅓ infuscated basally (Fig. 30). Scape and pedicel swollen, pedicel barrel shaped (Fig. 21). Frontal callus light brown. Mesoscutum gray green with black stripes . . . . . *tumidicornis*, n. sp.
– Hyaline triangle reaches vein R_{2+3}, apical spot narrowly enters 2nd submarginal cell, cells br and bm ½ and $\frac{1}{6}$ infuscated basally (Fig. 27). Scape and pedicel slightly swollen (Fig.18). Frontal callus reddish brown with black upper margin. Mesoscutum steel gray with black stripes . . . . . *pudicus* Osten Sacken
6. Abdominal tergites 1–2 light yellow to straw color, dark inverted "V" on tergite 2 compressed, not reaching beyond the middle of tergite 2. Flagellum 1.3 to 1.5 times longer than scape and pedicel combined 7
– Abdominal tergites 1–2 yellow, orange or light brown, inverted "V" pattern not compressed, extending beyond the middle of tergite 2 toward anterior margin. Flagellum equal to or up to 1.2 times longer than scape and pedicel combined 8
7. Fifth posterior cell infuscated, outer margin of crossband sinuous, cells br and bm ⅓ and ¼ infuscated basally (Fig. 28). Hind femur reddish-brown. Tergites 1–2 straw-colored, median anterior portion of tergite 2 with a greenish cast. Length 8–9.5 mm . . . . . *reicherti* Fairchild
– Fifth posterior cell hyaline, vein Cu_2 infuscated at border, outer margin of crossband straight or convex, cells br and bm ⅓ and $\frac{1}{5}$ infuscated basally (Fig.25). Hind femur dark brown. Tergites 1–2 yellow without a greenish cast. Length 6–8.5 mm . . . . . *dixianus* Pechuman
8. Hind femur yellow. Mesoscutum yellow with brown stripes. Outer margin of crossband straight or concave, cells br and bm ½ and ⅓ infuscated basally (Fig. 26). Scape and pedicel slightly swollen (Fig. 17). Length 8–10 mm . . . . . *flavidus* Wiedemann
– Hind femur dark brown basally. Mesoscutum yellow green with brown stripes. Outer margin of crossband straight, hyaline triangle slightly tinted, cells br and bm ⅓–½ and $\frac{1}{5}$ infuscated basally (Fig. 29). Scape and pedicel not swollen (Fig. 20). Length 5.7–7.5 mm . . . . . *sandyi*, n. sp.

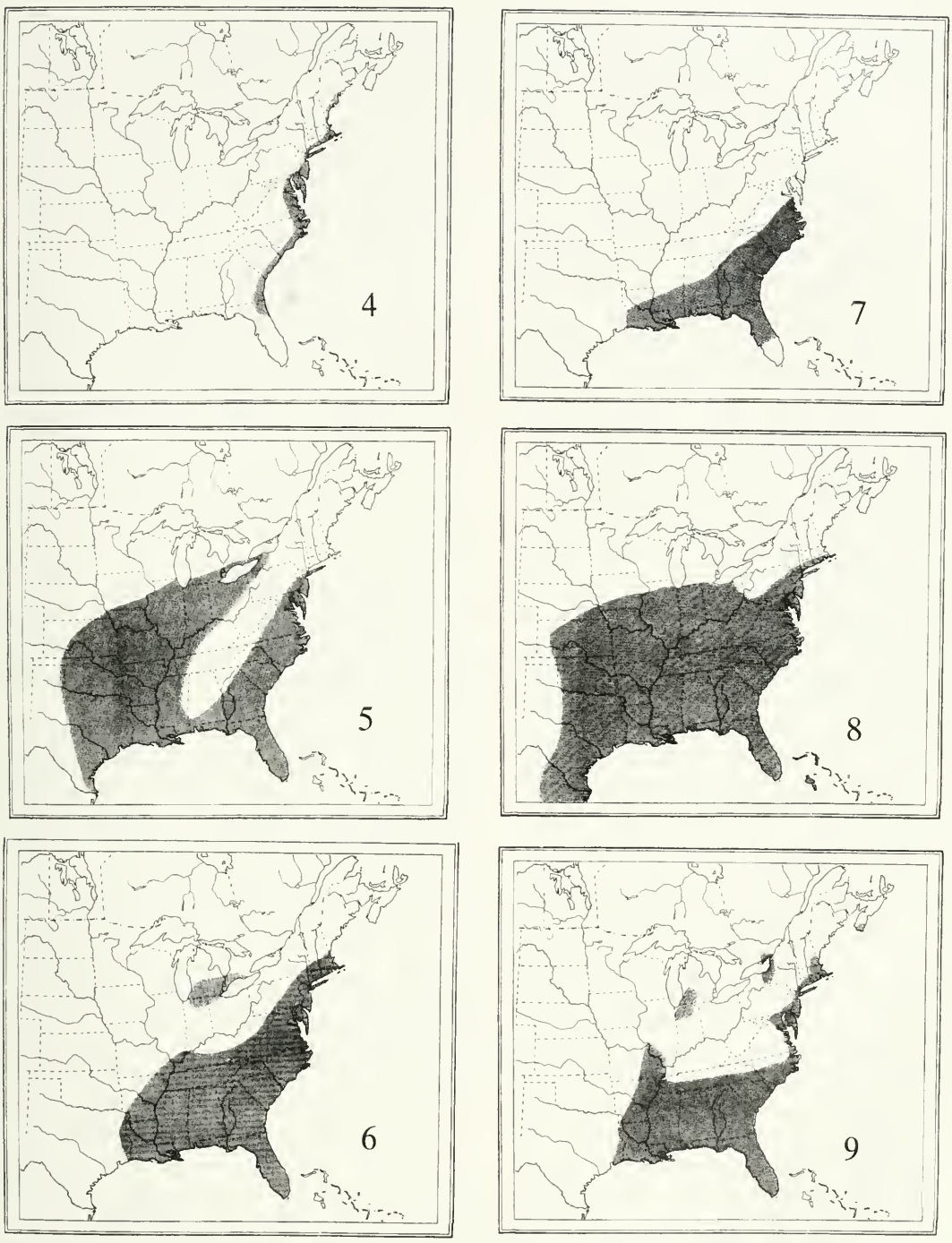
Chrysops atlanticus Pechuman (Fig. 4, 13, 22)

Chrysops canifrons Walker 1848: 197–198. Holotype female: Florida (BMNH). Senior synonym of *atlanticus*, suppressed by the International Commission on Zoological Nomenclature, Opinion No. 1711, 1993.

Chrysops atlanticus Pechuman 1949: 79–82. Holotype female: Rehoboth Beach, Delaware (CUIC); Jamback and Wall 1959: 23–24, description of egg, larva and pupa; Teskey 1969: 29–30, description of larva; Goodwin 1972: 104, description of pupa.

Diagnosis.—Length 6.5–9.2 mm. Scape and pedicel moderately swollen, flagellum equal to length of scape and pedicel combined. Mesoscutum grayish green in ground color. Wing pattern with smoky tinge, hyaline areas not clearly defined, hyaline triangle not extending beyond lower half of 1st submarginal cell.

Female.—Light to dark brown, length 8.5–9.2 mm. Scape and pedicel moderately swollen, light brown, basal flagellomere light brown, apical flagellomeres black, length of flagellum subequal to combined length of scape and pedicel, antennal ratio 15:10:25. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medially beneath tentorial pits to frontoclypeal suture. Maxillary palp brown with sparse black hairs. Frons yellow and gray tomentose with yellow hairs at vertex, width 1.13 times height. Frontal callus oblong, bulbous, light brown, width 1.54 times height. Vertex with glossy black integument surrounding shining brown ocelli. Mesoscutum grey green iridescent with three black longitudinal stripes, sublaterals



Figs. 4–9. Distributions. 4, *Chrysops atlanticus*. 5, *C. brunneus*. 6, *C. celatus*. 7, *C. dixianus*. 8, *C. flavidus*. 9, *C. pudicus*.

wider than median one, scutellum predominantly brown, lighter medianly. Legs predominantly yellow, hind coxa and fore tarusi brown, fore tibia with black hair, mid and hind tibia with mixed yellow and black hair. Wing pattern with usual hyaline areas smoky, apical spot broad, fading into 2nd submarginal cell, crossband brown with irregular outer margin, crossing 1st posterior cell at its center, a perpendicular line drawn from vein R_4 to hind margin of wing not forming line parallel to outer margin of crossband, hyaline triangle not extending beyond posterior ½ of 1st submarginal cell, discal cell, 4th and 5th posterior cells infuscated, 5th posterior cell paler in center, cells br and bm ¾ and ⅓ basally infuscated. Halter brown stalk yellow-brown knob. First abdominal tergite dark yellow, black haired medianly, tergites 2–5 with submedian oblique dark spots, gray posterior margin extending medianly into pale orange, equilateral triangle, dark spots on tergite 2 outline triangle and join anteriorly forming inverted "V" pattern, tergites 3–5 with submedian dark spots slightly separated anteriorly. Sternites 1–2 yellow, sternite 3 mottled yellow and brown, sternites 4–7 dark brown.

Male.—Similar to female except for usual sexual differences and following characteristics. Length 6.5–8 mm. Scape and pedicel slightly more enlarged with black hair that is longer and finer than on female. Mesoscutum sparsely covered with long yellow hair. Cell br entirely infuscated except for a subapical hyaline spot. Abdomen with yellow and black hair scattered over pattern.

Material examined.—934 ♀ and 18 ♂ examined from the following collections: CASC, CNCI, CUCC, CUIC, FMNH, FSCA, INHS, OSUC, TAMU, UGCA, UNHC, USNM.

Distribution.—Atlantic coast of North America from Maine to Florida. I have examined specimens from AL, DE, FL, GA, LA, MA, ME, MD, MS, NC, NH, NJ, NY, SC, TN, and VA. There are also published records for CT and RI.

Biology.—The larvae have been found in salt marsh and brackish pools. Based on their narrow distribution along the coast, they are probably restricted to this saline environment. Flight times for *C. atlanticus* are between April and September in Louisiana (Tidwell 1973), June to September in Virginia (Pechuman 1973), and late May to mid October in New York (Pechuman 1981). The adults are abundant during June and July throughout their range and are economically important due to their aggressive biting behavior. Thirty *C. atlanticus* bites were counted on 1 human in 90 seconds in a cultivated field near Cedarville, New Jersey, (Hansens, 1980). Anderson (1971) described *C. atlanticus* as being autogenous, depositing the first egg mass before seeking a blood meal. Subsequent work by Magnarelli and Anderson (1976) concluded that populations of *C. atlanticus* can be maintained by the first oviposition, making them difficult to control.

Chrysops atlanticus is not known to transmit any disease agent in nature; however, in the laboratory, tests have demonstrated it to be an effective experimental vector of the African filarial worm *Loa loa* (Orihel and Lowrie 1975).

Discussion.—*Chrysops atlanticus* is most similar to *C. sandyi,* C. *tumidicornis,* and to *C. brunneus,* based on the smoky wing pattern, association with a saline environment, and swollen antennae. *Chrysops atlanticus* differs from *C. brunneus* in its narrower scape and pedicel (Fig. 22) that when combined are equal in length to the flagellum, moderately inflated frontal callosity, grayish-green mesoscutum, and wing pattern without clearly defined hyaline areas. *Chrysops atlanticus* differs from *C. sandyi* in its larger size, blackish longitudinal stripes on the mesoscutum, and crossband with irregular outer margin. *Chrysops atlanticus* differs from *C. tumidicornis* in its larger size, less swollen pedicel, smokier wing pattern, and lighter abdominal pattern

that does not have a dark spot on tergite 1 under the scutellum. There appears to be no overlap in the geographical distribution of *C. atlanticus* with either *C. sandyi* or *C. tumidicornis.*

Color variation in *C. atlanticus* is common throughout its range, making it particularly difficult to define. The abdominal pattern can vary from tergites 2–6 having a pale inverted "V" formed by hair, to a dark, well defined, integumental inverted "V" pattern that includes ⅔ or more of the tergite. In all these cases, the characteristic wing pattern described above and the inflated scape and pedicel will define *C. atlanticus.*

Chrysops brunneus Hine
(Figs. 5, 14, 23)

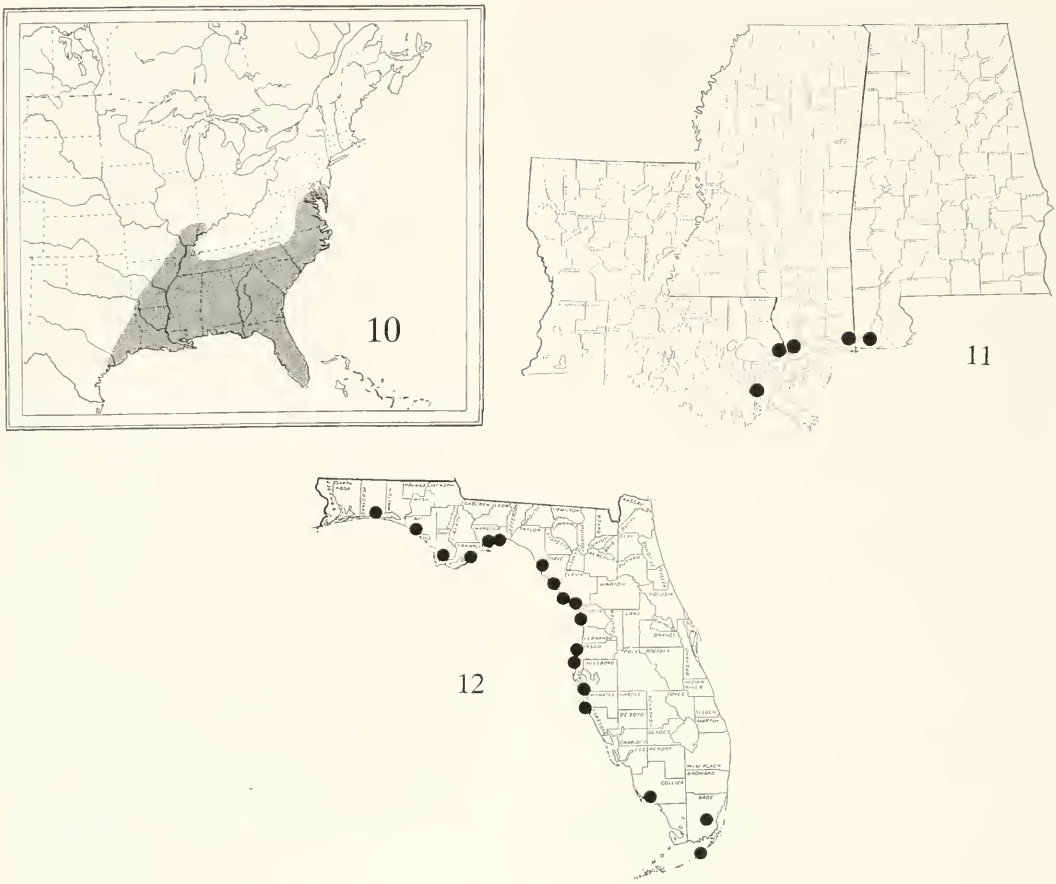
Chrysops brunneus Hine 1903: 34. Syntypes female and male: Sandusky, Ohio, ♀ ♂ (OSUC), 1 ♀ (BMNH); Goodwin 1976: 343, description of larva and pupa.

Diagnosis.—Robust species, length 8–10 mm. Antenna with scape and pedicel swollen, flagellum distinctly shorter than combined length of scape and pedicel. Frontal callus strongly inflated, width twice height. Wing with apical spot extensive, reaching around margin of wing to crossband and enclosing hyaline crescent. Cells br and bm ¾ and ½ infuscated basally. Abdominal pattern indistinct.

Female.—Yellowish brown. Scape and pedicel distinctly swollen, scape twice as long as broad, light brown, black setose, basal flagellomere yellow basally, dark brown apically, apical flagellomeres black, flagellum distinctly shorter than scape and pedicel combined, antennal ratio 18:12:25. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp light brown with sparse black hairs. Frons yellow tomentose with scattered yellow hairs, convergent above, height 1.3 times width at base. Frontal callus elliptical, distinctly narrowed laterally, strongly inflated, light brown, upper margin dark brown, width twice height. Vertex dark brown tomentose, except glossy around each ocellus, ocelli dark brown. Mesoscutum light brown tomentose and yellow pilose, except lateral margins pale yellow-gray tomentose, bearing 3 longitudinal stripes, median stripe very narrow, dark brown, sublateral stripes brown and broad. Scutellum dark brown basally, brown apically, yellow pilose. Pleuron yellow-gray tomentose. Fore coxa light brown tomentose, mid and hind coxa dark brown tomentose, femur, tibia and tarsus light brown, femur and tibia bearing yellow hairs, except apices of tibia bearing mixed yellow and black hairs, tarsus bearing black hairs. Wing pattern distinct, apical spot broad, extending around wing margin to crossband, leaving narrow hyaline band along outer margin of crossband that does not reach vein R_{2+3}, outer margin of crossband straight or sinuous, 5th posterior cell infuscated, cells br and bm ¾ and ½ their length respectively. Halter with dark brown stalk and light brown knob. Abdomen uniformly brown, lacking dark integumental markings, tergite 1 with black hair medianly, yellow hair laterally, tergites 2–4 predominantly black-haired, except for yellow hairs on posterior margin that expand medianly into indistinct yellow-haired triangles, tergites 5–7 with mixed black and yellow hairs forming no distinct pattern. Sternites 1–5 light brown, sternites 3–5 with progressively larger median and lateral brown integumental spots, 6–7 dark brown, all sternites with mixed black and yellow hairs.

Male.—Resembles female except for the usual sexual differences and the following characteristics. Length 8.2–10 mm, scape and pedicel slightly more inflated than in female, with longer, finer black hair, frontoclypeus with yellow tomentose triangle at vertex, cheeks yellow pollinose. Long yellow hairs scattered over mesoscutum, scutellum, and abdomen.

Material examined.—502 ♀ and 14 ♂



Figs. 10–12. Distributions. 10, *Chrysops reicherti.* 11, *C. sandyi.* 12, *C. tunidicornis.*

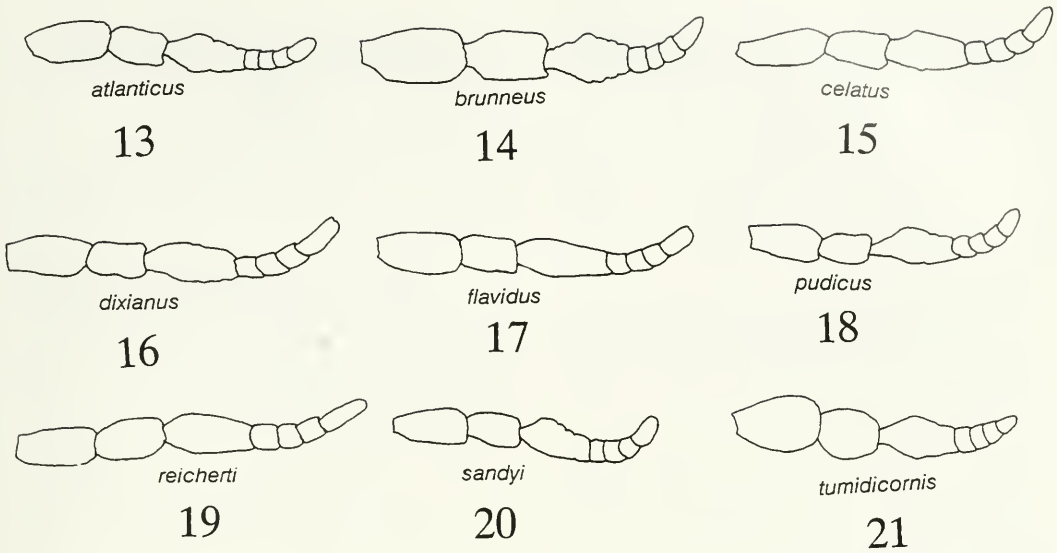
were examined from the following collections: AMNH, CASC, CNCI, CUCC, CUIC, FMNH, FSCA, INHS, OSUC, TAMU, UGCA, UNHC, USNM.

Distribution.—New York to Florida, west to Texas, and north to Michigan and southern Ontario. It is not found in the Appalachian Highlands and surrounding terrain. I have examined specimens from: AL, AR, DE, FL, GA, IL, IN, KS, KY, LA, MD, MI, MS, NJ, NY, OH, OK, PA, SC, TN, TX, and VA. It is also known from IA, MO, NC, and Ontario, Canada.

Biology.—*Chrysops brunneus* is associated with both fresh and salt water habitats. Goodwin (1976) reared a larva of this species collected from a salt marsh in McClellanville, SC. Adults are commonly found in marshes near lakes such as Lake Michigan, Lake Erie and Lake Ontario.

Discussion.—*Chrysops brunneus* is very distinctive and can be separated from other species of the *C. flavidus* group by its strongly inflated scape and pedicel that combined are longer than the flagellum, and by its reduced hyaline triangle appearing as a crescent-shaped area between the crossband and broad apical spot. The smoky wing pattern of *C. brunneus* and its presence in a saline environment are similar to that of *C. atlanticus,* but is easily separated by those characters noted above.

The only variation observed in this species was the abdominal pattern that has tergites 2–3 with small, median, black dashes on the integument in approximately 5% of



Figs. 13–21. Female antennae. 13, *Chrysops atlanticus*. 14, *C. brunneus*. 15, *C. celatus*. 16, *C. dixianus*. 17, *C. flavidus*. 18, *C. pudicus*. 19, *C. reicherti*. 20, *C. sandyi*. 21, *C. tumidicornis*.

the specimens examined. Ordinarily the abdominal pattern is indistinct with only some dark shadowing from dark hairs.

Chrysops celatus Pechuman
(Figs. 6, 15, 24)

Chrysops flavidus celatus Pechuman 1949: 82–83. Holotype female: Medford Lakes, New Jersey (CUIC); Pechuman 1957: 30, description of male.

Chrysops celatus: Teskey 1969: 34, description of larva and pupa.

Diagnosis.—Black and yellow, length 8–9.8 mm. Scape and pedicel not swollen, flagellum ⅓ longer than scape and pedicel combined. Frontal callus spade shaped, width and height subequal. Mesoscutum greenish gray iridescent with black longitudinal stripes. Cells br and bm ½ and ⅕ infuscated basally.

Female.—Scape and pedicel not swollen, light brown, black setose, basal flagellomere light brown basally, black apically, apical flagellomeres black, 1.3 times length of basal flagellomere, antennal ratio 15:10:34. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp and labrum yellow. Frons predominantly yellow-gray tomentose with scattered yellow hair, slightly convergent above, height 1.5 times width at base. Frontal callus spade shaped, bulbous, yellow brown, width and height subequal. Vertex gray tomentose, except glossy brown integument associated with each ocellus which extends narrowly to upper margin of frontal callus. Mesoscutum greenish-gray iridescent, except lateral margins yellow tomentose, bearing 3 black longitudinal stripes, the median one narrow and flanked with gray. Scutellum black basally. Pleuron yellow tomentose. Legs mostly yellow, fore leg with tarsus and apical portion of tibia dark brown with black hair, mid and hind coxa brown, tarsus with black hairs. Wing pattern with broad apical spot entering apical half of 2nd submarginal cell, apex of hyaline triangle not reaching vein R_{2+3}, outer margin of brown crossband sinuous, 5th posterior cell infuscated basally, hyaline apically, cells br and bm ½ and ⅕ infuscated basally. Halter brown. Tergites 1–2 yellow brown, tergite 2 with darker median integumental marking appearing as an inverted "V" set over median yellow-

brown triangle, tergites 3–4 predominantly brown except for lighter posterior margin that expands medianly into light brown pollinose triangle, remaining tergites with anterior ⅔ brown, posterior ⅓ yellow-brown. Sternites yellow-brown pollinose with sternites 3–7 bearing narrow yellow pollinose line along the posterior margin, sternites 5–7 predominantly brown.

Male.—Similar to female except for the usual sexual differences and following characters. Length 6.5–7.5 mm. Pedicel only slightly shorter than scape, with finer, longer black hairs, length of basal flagellomere and combined apical flagellomeres subequal. Apical spot reaches posterior half of 2nd submarginal cell and then fades along hind margin, cells br and bm ¾ and ½ infuscated basally. First tergite with dark spot under scutellum or entirely dark. Fifty percent of males examined with abdominal pattern of yellow and black with a black scutellum.

Material examined.—574 ♀, 30 ♂, examined from the following museums: AMNH, CASC, CNCI, CUCC, CUIC, FSCA, INHS, TAMU, UGCA, UNHC, USNM.

Distribution.—Massachusetts south to Florida, west to Texas; disjunct population in Michigan, southern Ontario, and northern Ohio, Illinois, and Indiana. I have examined specimens from the following states: AL, CT, DE, FL, GA, IN, KY, LA, MA, MD, MI, MS, NC, NH, NJ, NY, SC, TN, TX, and VA. L. L. Pechuman has recorded specimens from WV, and Ontario, Canada.

Biology.—Teskey (1969), based his description of the larva on 35 specimens. They were collected from 3 sites with fresh, standing water: wet sand, organic soil, and around roots of aquatic vegetation. In 1972, Teskey also collected larvae from the edge of a slow-moving stream in Virginia (Pechuman 1973).

The flight period for *Chrysops celatus* is late May to September in its northern range, and from April to late October in the south. Peak flight time over its entire range is in June. Although it is a common species, it is not abundant enough to be considered a pest.

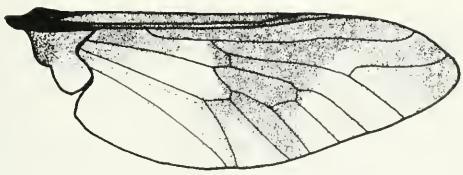
Discussion.—Pechuman (1949) first described *C. celatus* as a subspecies of *C. flavidus*, and it was so treated until Teskey (1969) found the larvae and pupae of the two subspecies to be specifically distinct. The adult of *C. celatus* most closely resembles *C. flavidus* and *C. reicherti,* and can be separated by its greenish-grey mesoscutum and the longer, more slender antennae. The sinuous outer margin of the crossband in *C. celatus* is similar to that of *C. reicherti,* but in *C. flavidus* this margin is either straight or concave. The larva resembles *C. flavidus* (Goodwin 1976) and *C. dixianus* (Teskey 1969).

The characters used to define *C. celatus* are consistent, in most cases, but there is some variation in the color pattern of the abdomen and wings, and in the color of the scutellum. The abdominal pattern on tergites 2–3 may vary from a black inverted "V" on the integument to lighter markings of dark hairs only. The apical spot of the wing may be extended and fade out along the hind margin of the wing, approaching a pattern much like that of *C. reicherti.* Specimens with this wing pattern tend to be more robust and have a more darkly infuscated wing. The scutellum, which is usually dark basally and reddish apically, is either wholly dark or reddish.

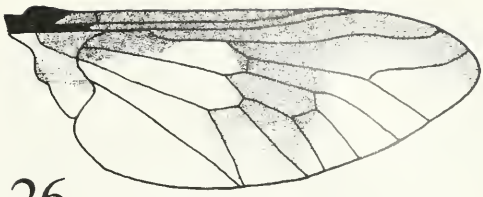
Chrysops dixianus Pechuman
(Figs. 7, 16, 25)

Chrysops dixianus Pechuman 1974: 185–187. Holotype female: Wedge Plantation, McClellanville, South Carolina (CUIC); Goodwin 1976: 345–347, description of larva and pupa.

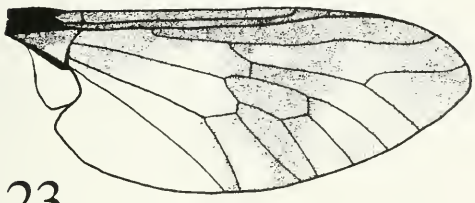
Diagnosis.—Yellow and brown species, length 6–8.5 mm. Antenna not swollen, flagellum ⅓ longer than scape and pedicel combined. Frons width at base subequal to width at vertex. Hind coxa and femur dark



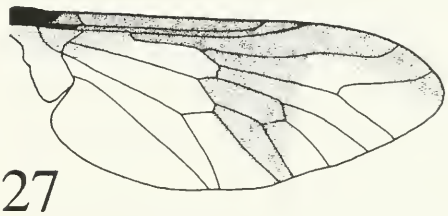
22 atlanticus



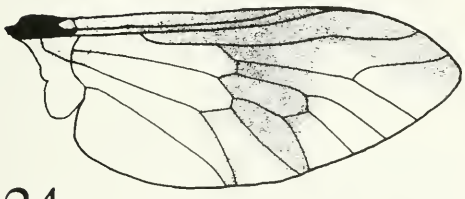
26 flavidus



23 brunneus

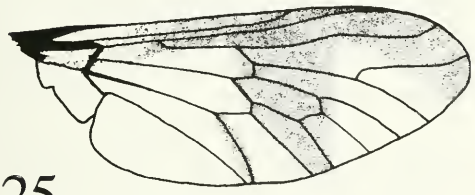


27 pudicus

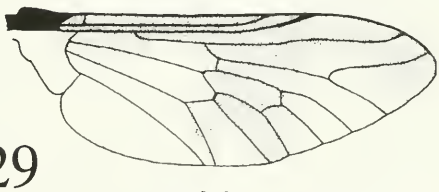


24 celatus

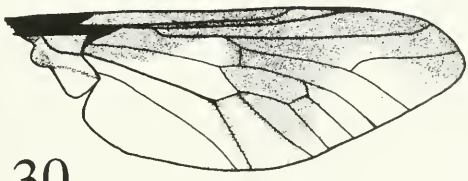
28 reicherti



25 dixianus



29 sandyi



30 tumidicornis

Figs. 22–30. Female wing patterns. 22, *Chrysops atlanticus*. 23, *C. brunneus*. 24, *C. celatus*. 25, *C. dixianus*. 26, *C. flavidus*. 27, *C. pudicus*. 28, *C. reicherti*. 29, *C. sandyi*. 30, *C. tumidicornis*.

brown. Wing picture with 5th posterior cell hyaline, infuscated area bordering vein Cu_2.

Female.—Scape and pedicel not noticeably enlarged, yellow with black setae, basal flagellomere yellow basally, remainder brown, apical flagellomeres dark brown to black, flagellum approximately ⅓ longer than length of scape and pedicel combined, antennal ratio 13:9:32. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp light brown with sparse black hair basally, more dense apically. Frons grayish-yellow pollinose with scattered yellow hairs, width at base subequal to width at vertex, height 1.15 times width at base. Frontal callus oval, slightly inflated, light brown, width 1.4 times height. Vertex yellow gray, glossy surrounding each ocellus, ocelli yellow. Mesoscutum yellow-gray tomentose in ground color with 3 dark brown longitudinal stripes, median one flanked with lighter shade of brown, the two sublateral stripes merge with median one near the scutellum, yellow hair scattered over entire mesoscutum. Scutellum dark brown basally, light brown apically. Pleuron yellow-gray tomentose. Fore coxa and femur yellow, fore tibia with basal ½ yellow, apical ½ and fore tarsus dark brown, bearing black hair. Mid coxa dark brown, femur, tibia and metatarsus yellow, remainder of tarsus dark brown. Hind coxa and femur dark brown, tibia light brown basally, darkening to apex, metatarsus light brown, remaining portion of tarsus dark brown, tibia and tarsus bearing stiff black hair. Wing pattern distinct, apical spot broad, filling half of 2nd submarginal cell, hyaline triangle not quite reaching vein R_{2+3}, outer margin of crossband straight or convex, 5th posterior cell hyaline, vein Cu_2 infuscated along border, cells br and bm ⅓ and ⅕ infuscated basally respectively. Halter with stalk brown, knob dark brown. Abdominal pattern distinct, tergite 1 yellow, light brown under scutellum, tergite 2 with anterior half entirely yellow, posterior half yellow with 2 median oblique dark brown dashes making a flattened inverted "V" not reaching posterior margin of tergite, posterior margin with median yellow triangle and 2 submedian brown spots, tergite 3 with wide dark brown band that narrows medianly, not reaching anterior or posterior margins, posterior margin yellow, tergites 4–5 with anterior ⅔ dark brown, remaining ⅓ yellow, tergites 6–7 dark brown. Sternites 1–4 yellow, 4th sternite with dark brown median spot, 5th sternite brown with yellow hind margin, remaining sternites dark brown.

Male.—Not previously described. Length 7.4 mm. Scape and pedicel not noticeably enlarged, yellow with black hair, basal flagellomere yellow at base, remainder brown, apical flagellomeres black, antennal ratio 15:12:34. Maxillary palp yellow with long yellow hair and a few black hairs, length twice width. Mesoscutum yellow-gray tomentose, above wing bases yellow tomentose, with 3 dark brown longitudinal stripes that merge at the base near the scutellum. Scutellum dark brown at base, reddish brown apically. Fore coxa and femur yellow, tibia with basal ½ yellow, apical ½ and tarsus dark brown, bearing black hair. Mid coxa dark brown, femur, tibia and metatarsus yellow, remainder of tarsus dark brown. Hind coxa and femur dark brown, tibia light brown basally, darkening to apex, metatarsus light brown, remaining portion of tarsus dark brown, tibia and tarsus bearing stiff black hair. Wing pattern with cells br and bm ½ and ¼ infuscated basally, hyaline triangle reaching vein R_{2+3}, infuscated area bordering Cu_2 vein wider than in female. First abdominal tergite yellow, with light brown shading under scutellum, 2nd tergite with anterior ½ yellow, posterior ½ with 2 median oblique dark brown dashes not attaining posterior margin of tergite, posterior margin with vague, median yellow triangle, tergite 3 with wide dark brown median band not reaching anterior or posterior margins, bordered laterally by black setae, hind margin

yellow, tergites 4–5 with anterior ⅔ dark brown, remaining ⅓ yellow, tergites 6–7 dark brown. Sternites 1–3 yellow, the 3rd sternite with a dark brown median spot, sternites 5–6 brown with yellow hind margin, remaining sternite dark brown. Based on 1 specimen from Alachua Co. Florida, collected by G. B. Fairchild, V-24/25-1975, (FSCA).

Material examined.—468 ♀, 1 ♂, examined from the following museums: AMNH, CNCI, CUCC, CUIC, FSCA, INHS, TAMU, UGCA, UNHC, USNM.

Distribution.—Virginia to Florida, west to Louisiana and Arkansas. I have examined specimens from: AL, AR, FL, GA, LA, MS, NC, and SC. L. L. Pechuman has locality data from VA.

Biology.—Little is known about the biology of *Chrysops dixianus*. The larva was taken from the edge of a freshwater lake in mud and decomposing leaves (Goodwin 1976). Pechuman (1974) stated that *C. dixianus* could be a common pest, as suggested by 124 specimens collected on July 6, 1971, in Berkeley County, South Carolina, by D. C. Sheppard.

Discussion.—This species was once confused with *C. pudicus* but differs in having a longer, thinner flagellum, a brown mesoscutum, and the anterior portion of tergite 2 without markings. The adult of *C. dixianus* appears most similar to *C. reicherti*. The 2nd abdominal tergite of both has markings only on the posterior ½, but *C. dixianus* is smaller, has a defined apical spot, and the 5th posterior cell is hyaline.

There is little variation in this species. The mesoscutum, normally with a narrow median brown stripe, may have the stripe as wide as the two sublaterals. The scutellum may be all dark, and the abdominal markings on tergites 2–3 can vary from median dashes to a more extensive pattern reaching the lateral margins. The hind femur can be up to ½ light brown.

Chrysops flavidus Wiedemann
(Figs. 8, 17, 26)

Chrysops flavidus Wiedemann 1821: 55. Holotype female: Savannah, Georgia (MZLU); Kröber 1926: 291–292, redescription; Teskey 1969: 39, description of larva and pupa.

Chrysops pallida Macquart 1838: 162 (1838: 166). Holotype female: locality unknown (MNHN). Synonomized by Philip 1965: 325.

Chrysops pallidus Bellardi 1859: 73. Holotype female: Mexico (MRSN). Preoccupied by Macquart 1838.

Chrysops guiterasi Brunetti 1923: 401. Syntypes female and male: Manzanillo, Cuba, ♀ (BMNH), ♂ (ZMHB). Synonomized by Bequaert, 1940: 279.

Diagnosis.—Light brown, length 8–10 mm. Scape and pedicel slightly swollen. Mesoscutum yellow with brown stripes. Hind margin of crossband straight or concave, cells br and bm ½ and ⅓ infuscated basally.

Female.—Scape slightly enlarged, scape and pedicel light brown, black setose, basal flagellomere light brown, apical flagellomeres black, equal to or longer than basal flagellomere, antennal ratio 15:10:30. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal sutures. Maxillary palp and labrum yellow. Frons predominantly yellow tomentose, slightly convergent above, height 1.28 times width at base. Frontal callus oblong, bulbous, light brown, width 1.83 times height. Vertex yellow tomentose, except glossy around each ocellus, ocelli black. Mesoscutum yellow tomentose, yellow pilose, bearing three subshiny brown longitudinal stripes, median one narrower than the sublaterals. Scutellum yellow basally, orange-yellow apically. Pleuron yellow tomentose. Legs predominantly yellow, mid and hind coxa brown, hind tibia with scattered black hair apically, fore, mid, and hind tarsi with black hair. Wing pattern with clearly defined hyaline areas, apical spot entering posterior half of 2nd submarginal cell, apex of hyaline triangle not quite reaching vein R_{2+3}, outer margin of cross-

band straight or slightly concave, 5th posterior cell infuscated basally, hyaline apically, cells br and bm ½ and ⅓ infuscated basally. Halter with brown knob and yellow stalk. Abdominal tergites golden brown, tergites 2–5 with median yellow pollinose triangles, each triangle outlined submedianly with indistinct brown spots, first tergite with two submedian brown spots, hind margin of tergites 3–6 narrowly yellow tomentose, tergites bearing mixed black and yellow hairs. Sternites golden yellow tomentose, sternites 2–6 bearing a narrow yellow posterior border, sternites 4–5 with median indistinct brown spot.

Male.—Similar to female except for the usual sexual differences and the following characters. Length 6.5–7.2 mm. Scape and pedicel with longer, finer, black hair. Wing faintly tinted below the apical spot and along the hind margin, basal ½ of cell br infuscated. Abdomen without distinct median triangles.

Material examined.—1,245 ♀, 75 ♂ examined from the following museums: AMNH, BMNH, CASC, CNCI, CUCC, CUIC, FMNH, FSCA, INHS, OSUC, TAMU, UGCA, UNHC, USNM.

Distribution.—Missouri to Massachusetts south to Texas, Florida, Mexico, the Bahamas, Belize, and Cuba. I have examined specimens from AL, AR, DE, FL, GA, IL, IN, KS, LA, MA, MD, NC, NJ, NY, OK, SC, TN, TX, VA, Belize, the Bahamas, and Cuba. L. L. Pechuman recorded specimens from CT, IA, KY, MO, MS, OH, PA, RI, WV, and Mexico.

Biology.—The larva described by Teskey (1969) was taken from sand on the edge of a pond. Tidwell (1973) collected most of the Louisiana specimens from the banks of ponds and waterways in bottomland hardwood forests associated with the Mississippi flood plain. Jones and Bradley (1923) reared a larva found at the bottom of a brook. Jones and Anthony (1964) collected larvae from the margins of brackish water and from highly alkaline soil and reared 38 specimens whose pupal period averaged 8 days.

Adults in northern regions, are active from June to October and most abundant in July. In the south they fly as early as March and continue until late September. In some areas of Florida there are two distinct population peaks of *Chrysops flavidus,* one occurring in April and May, the other in August and September (Jones and Anthony 1964).

This species was described as pestiferous to humans (Hine 1906, Jones and Anthony 1964), generally attacking the head and neck, and considered one of the worst "stock pests" in the genus *Chrysops* (Hine 1906).

Discussion.—*Chrysops flavidus* is most commonly confused with *C. atlanticus, C. reicherti* and *C. celatus,* all considered at one time to be either subspecies or varieties of *C. flavidus.* It is also similar to *C. sandyi,* described below. *Chrysops flavidus* differs from *C. atlanticus* in having thinner antennae, a yellow mesoscutum, and a wing pattern with well defined hyaline areas. *Chrysops flavidus* differs from *C. celatus* in its shorter, stouter antennae, yellow mesoscutum, straight or slightly concave outer margin of the crossband, and its less distinct abdominal pattern. It differs from *C. reicherti* in having the outer margin of the crossband straight or slightly concave, yellow hind femur, and an inverted "V" pattern that reaches the anterior half of tergite 2. *Chrysops flavidus* differs from *C. sandyi* in its larger size, yellow mesoscutum with dark brown stripes, and its more divergent frons with the width at the vertex greater than the width of the basal callus.

Variation in *C. flavidus* is found in the tinting of the wing and in the abdominal color pattern. Approximately 10% of the specimens examined had tinting of the wing below the apical spot, approaching the smoky wing pattern of *C. atlanticus.* However, *C. flavidus* has a consistently straight or slightly concave outer margin of the crossband and yellow mesoscutum. Speci-

mens with the apical portion of the wing tinted have been collected from the coastal areas of South Carolina, Georgia, and Florida. A collection of 27 specimens from Monroe County, Florida, exhibit a tinted wing, have a stouter scape, a grayer mesoscutum, and a reddish brown abdomen. Other than these differences, these specimens do not vary in size and other characters.

The female syntype of *Chrysops guiterasi,* described from Cuba and considered a synonym of *C. flavidus,* was examined. I have no doubt it is conspecific with *C. flavidus,* although the abdomen is reddish-brown.

Chrysops pudicus Osten Sacken
(Figs. 9, 18, 27)

Chrysops pudicus Osten Sacken 1875: 381–382. Lectotype female: Beverley, Massachusetts, (MCZC). Lectotype examined, missing head; Goodwin 1976: 350–351, description of pupa.

Diagnosis.—Brown and black, length 6.5–8.2 mm. Frontal callus reddish-brown with black upper margin. Mesoscutum steel gray with black stripes. Hyaline triangle reaches vein R_{2+3}, apical spot narrowly enters 2nd submarginal cell. Cells br and bm ½ and ⅙ infuscated basally.

Female.—Scape and pedicel slightly swollen, ground color shiny brown, bearing stiff black hairs, basal flagellomere light brown gradually darkening at apex, apical flagellomeres black, flagellum subequal to length of scape and pedicel combined, antennal ratio 13:9:23. Frontoclypeus glossy reddish brown, eye margins bearing light brown tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp yellow. Frons light brown tomentose, yellow pilose, slightly convergent above, length 1.3 times width at base. Frontal callus oblong, bulbous, reddish brown with black upper margin, margin concolorous with smooth integument surrounding ocelli. Vertex dark brown, glossy around each ocellus, ocelli black. Scutellum black. Fore coxa light brown, trochanter slightly darker, femur light brown, apical ¼ darker brown, tibia with black hair apically, tarsi black, mid coxa dark brown, femur light brown with scattered stiff yellow hair, tibia light brown with short black setae apically, tarsus light brown basally, dark brown apically, covered with black setae, hind femur dark brown with yellow hair, tibia light brown with yellow hair basally, remainder with yellow and black hair, tarsus light brown basally, black apically. Wing pattern with clearly defined hyaline areas, apical spot narrow, entering extreme apical portion of 2nd submarginal cell, hyaline triangle reaches vein R_{2+3}, outer margin of crossband straight or slightly concave from vein R_{2+3} to vein M_3, cell br and bm ½ and ⅙ infuscated basally. Abdomen with first 2 segments yellow, 1st tergite with large black spot under scutellum not reaching posterior margin, extending laterally to approximately ½ width of tergite, 2nd tergite with black integumental inverted "V" not reaching anterior or posterior margin, black hair scattered over black integumental pattern, orange median triangle under black inverted "V" pattern, tergites 3–4 black anteriorly with median orange triangle posteriorly, black pattern not reaching lateral margin of the tergite, tergites 5–6 black anteriorly, yellow posteriorly. Abdomen yellow ventrally, sternites 3–4 with median black spot, spot on sternite 3 smaller than on sternite 4, remaining sternites black.

Male.—Similar to female except for the usual sexual characteristics and the following characters. Scape and pedicel covered with long, fine, black hair. Mesoscutum almost entirely black, the 3 stripes indistinct, with scattered yellow hair. Apical spot slightly more extensive. Cell br ¾ infuscated basally.

Material examined.—91 ♀, 1 ♂ examined from the following collections: CUIC, FSCA, UNHC.

Distribution.—Southern Illinois to Mas-

sachusetts, south to eastern Texas and Florida with some disjunct populations in northern Indiana, Michigan, New York, southern Ontario, and Nova Scotia. I have examined specimens from AL, CT, FL, GA, LA, LA, NC, NH, NY, RI, SC, and Nova Scotia. L. L. Pechuman has records from NJ, DE, IN, IL, MD, MI, MS, OK, TN, TX, and WI.

Biology.—The larva of this species, although not formally described, has reportedly been taken from wet soil along a roadside ditch (Jones and Anthony 1964, Pechuman 1973). The pupa was described by Goodwin (1976) from Baldwin County, Alabama, but the habitat is unknown. Jones (1953) indicated that in parts of Florida there are two generations of *C. pudicus* annually, one that emerges in May–June and another in August–September. Large numbers can occur in wooded areas of Florida during April and May (Jones and Anthony 1964).

Discussion.—Pechuman et al. (1983) treated *C. pudicus* as a member of the *Chrysops callidus* group, which includes *C. dimmocki* Hine, a species that can resemble *C. pudicus*. Members of the *C. callidus* group all have a black frontal callus, inverted "V" pattern on 2nd abdominal tergite that reaches the anterior margin and, in some species, a hyaline triangle that extends beyond vein R_{2+3}. *Chrysops pudicus* differs from members of the *C. callidus* group in having an abdominal pattern on tergite 2 not reaching the anterior margin, a hyaline triangle not crossing vein R_{2+3}, and a yellow frontal callus with dark top margin. The frontal callus is rarely entirely dark (Brennan 1935, Teskey 1990), and the hyaline triangle rarely reaches beyond vein R_{2+3}. Therefore, I have chosen to place *C. pudicus* in the *Chrysops flavidus* group.

Chrysops pudicus most closely resembles *C. tumidicornis*, described below, in having similar size, dark coloration, and 1st abdominal tergite with a dark spot under the scutellum. They differ in that *C. pudicus* has a narrower scape and pedicel, a less extensive, well defined apical spot, and a hyaline triangle that reaches R_{2+3}.

Variation within *C. pudicus* occurs in the extent of the hyaline triangle (Pechuman 1973) and in the color of the frontal callus. Of the 91 females examined, 10 specimens from Florida had a hyaline triangle that did not reach vein R_{2+3}. Although variation in color of the frontal callus is mentioned in various publications (Brennan 1935, Teskey 1990), all the specimens I examined had a yellow frontal callus with a dark upper margin.

Chrysops reicherti Fairchild
(Figs. 10, 19, 28)

Chrysops reicherti Fairchild 1937: 60–61. Holotype female: Monticello, Jefferson County, Florida (MCZC). Holotype examined. Goodwin 1972: 105–107, description of larva and pupa.

Chrysops flavida reicherti: Philip, 1947: 273, treated as a subspecies. Pechuman 1957: 30–31, description of male; Philip 1965: 325, treated as a variety of *C. flavidus.*

Diagnosis.—Yellow and brown, length 8–9.5 mm. Antenna not swollen. Mesoscutum yellow in ground color with 3 brown stripes. Tergites 1–2 light yellow, darker pattern on posterior half of tergite 2. Cells br and bm are ⅓ and ¼ infuscated basally.

Female.—Scape and pedicel not swollen, light brown with black setae, flagellum black, antennal ratio 15:10:35. Frontoclypeus glossy yellow, eye margins bearing grayish yellow tomentum extending medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp brown. Frons yellow tomentose, slightly convergent above, height 1.3 times width at base. Frontal callus oblong, bulbous, light brown, width 1.33 times height. Vertex light brown around each ocellus, ocelli yellow. Mesoscutum yellow tomentose with three subshiny brown longitudinal stripes, median one narrower than sublaterals, flanked with

lighter shade of brown. Scutellum yellow brown. Pleuron yellow tomentose. Legs predominantly light brown, fore and mid tarsi brown, mid and hind tibiae with dark hair apically, hind femur reddish brown, apical tarsomeres brown to black. Wing with extensive apical spot reaching posterior ½ of 2nd submarginal cell fading into 3rd posterior cell, hyaline triangle not reaching vein R_{2+3}, outer margin of crossband bowed outward at center, 5th posterior cell infuscated basally and along vein margins, hyaline apically, cells br and bm ⅓ and ¼ infuscated basally. Halter with brown stalk and knob. First abdominal tergite light brown, second tergite with basal half yellow, green tinted medianly, apical half with oblique brown spots reaching hind margin and enclosing pale triangle. Tergite 3 with brown median band set over median orange triangle, hind margin of tergite gray. Tergites 4–6 with basal half brown, apical half yellow. Sternites predominantly golden brown, 3–6 with median brown spot progressively enlarged on posterior segments.

Male.—Similar to female except for the usual sexual differences and the following characters: Length 6.5–7.0 mm. Scape swollen, pedicel ⅕ longer than in female, scape and pedicel with longer, finer, black hair. Mesoscutum with long yellow hair. Wing with apical spot more extensive, cells br and bm ½ and ⅓ infuscated basally.

Material examined.—720 ♀, 20 ♂ examined from the following collections: CASC, CNCI, CUIC, FSCA, INHS, TAMU, UGCA, UNHC, USNM.

Distribution.—Southern Illinois to Delaware, south to eastern Texas and Florida. I have examined specimens from AL, AR, FL, GA, IL, KY, LA, MA, MD, MS, NC, SC, TN, TX, and VA. L. L. Pechuman has records from IN and MO.

Biology.—The larvae of *Chrysops reicherti* have been collected in very wet mud and organic debris from small ponds and lakes (Goodwin 1972, Tidwell 1973). Adults have been collected between April and September in the southern states. The one Massachusetts specimen was collected on May 8.

Discussion.—*Chrysops reicherti* was originally described as a species by Fairchild (1937). Philip (1947) listed it as a subspecies of *C. flavida.* Goodwin (1972), after describing the larva and pupa of *C. reicherti* and comparing them to those of *C. flavidus,* considered them separate species and elevated *C. reicherti* to a full species.

Chrysops reicherti is most commonly confused with *C. flavidus,* but is separated by its pale yellow first two abdominal segments, sinuous outer margin of the crossband, and the slightly darker hind femora. In the key above, *C. reicherti* shares with *C. dixianus* the color pattern on the posterior portion of the second tergite. They differ in that *C. dixianus* has a straighter outer margin of the crossband, an apical spot that reaches slightly beyond the apex of the wing, and 5th posterior cell extensively hyaline.

Variation in *C. reicherti* includes tinting in the usual hyaline areas of the wing, 2nd abdominal tergite without the greenish cast described by Fairchild and, hind femur light or dark brown.

Chrysops sandyi Baier, new species
(Figs. 12, 20, 29)

Diagnosis.—Yellow and brown, length 6–8 mm. Antenna slightly enlarged. Mesoscutum with brown iridescent stripes. Wing slightly tinted in usual hyaline areas. Cells br and bm are ½ and ⅓ infuscated basally.

Holotype female.—Length 6.2 mm. Scape slightly enlarged, antenna light brown except apical 3/4 of 1st flagellomere slightly darker, apical 4 flagellomeres black, antennal ratio 13:9:24, length of flagellum subequal to combined length of scape and pedicel. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp light brown with sparse black hairs, length 4 times width. Frons yellow tomentose with

scattered yellow hairs, convergent above, height slightly more than width at base, width at vertex less than width of frontal callus. Frontal callus oval, yellow brown, width 1.7 times height. Vertex yellow tomentose, glossy around each ocellus, ocelli light brown. Mesoscutum yellow-green iridescent tomentose, except lateral margins iridescent yellow gray, bearing 3 brown to dark brown stripes, the median one darker and narrower than the two sublaterals. Scutellum dark brown basally, brown apically. Pleuron yellow gray. Legs mostly light brown, fore tarsus black, apical portion of tibia dark brown with black hair, mid coxa dark brown, tarsus with black hair, hind coxa dark brown, femur and basal tibia reddish brown, apical tibia brown, apical tibia and tarsus with black hair. Wing with broad apical spot reaching posterior half of 2nd submarginal cell, apex of hyaline triangle including posterior half of 1st submarginal cell, not reaching vein R_{2+3}, outer margin of crossband straight, 5th posterior cell slightly tinted, infuscated along vein Cu_2, cells br and bm ½ and ⅓ infuscated basally. Halter with light brown stalk and brown knob. Tergites 1–2 yellow brown, tergite 1 with a few dark hairs under scutellum, tergite 2 with a median brown integumental marking appearing as a flattened inverted "V", not reaching anterior margin, fading into pale posterior margin, median orange-brown triangle behind inverted "V" pattern, tergite 3 mottled dark brown anteriorly, orange brown posteriorly, extending medianly to form orange triangle, tergites 4–6 dark brown anteriorly, yellow orange posteriorly, tergites 3–6 with gray hind margin. Sternites 1–3 yellow brown, sternite 3 bearing a median brown spot, sternites 4–7 dark brown, posterior margin pale yellow tomentose.

Male.—Unknown

Material examined.—Holotype ♀, ALABAMA: Mobile County, VII-1952, T. R. Adkins (CUIC). Paratypes: 105 ♀. ALABAMA: Mobile County, VII-1952 (62 ♀), VII-24-1952 (4 ♀), T. R. Adkins (CUIC); 1 ♀ Corden, VII-8-1962, M. Tidwell (FSCA). LOUISIANA: St. Tammany Parish, 4 ♀ Slidell, 7 mi SE,VI-23-1980, E. A. Lisowski (CUIC). MISSISSIPPI: Hancock County, Ansley, VI-10-1966 (5 ♀), VI-20-1966 (6 ♀), Diamond & Bradford (FSCA); 2 ♀ V-5-1976, M. Tidwell (FSCA); 1 ♀ Pearlington, VI-9-1966, ? collector (FSCA); 1 ♀ MTO fee area, IV-27-1965, R. Hepburn (FSCA). Jackson County, Fountainbleau, VI-26-1966 (2 ♀), VII-27-1968 (1 ♀), B. Byrd (FSCA); 4 ♀ Gautler, 4.5 mi WSW, VI-24-1980, E. A. Lisowski (CUIC); 12 ♀ Ocean Springs, V-10-1970, G. Ross (FSCA).

Etymology.—Named in honor of G. B. "Sandy" Fairchild for his extensive contribution to the organization of *Chrysops* taxa and his desire to see the southeastern species clarified. His examination of specimens and critical comments on this work has been greatly appreciated.

Distribution.—Gulf coast of Alabama, Mississippi, and Louisiana.

Biology.—*Chrysops sandyi* has been collected between April 27 and August 8. Based on its distribution along the Gulf coast, it is probably limited to a litoral environment.

Discussion.—This species has been confused with *C. atlanticus* because of the tinted wing and greenish iridescent color of the mesoscutum. *Chrysops sandyi* has a narrower antennae, the pedicel ¾ the length of the scape, longer palpi, length 4 times width of apical palpomere, mesoscutum with brown longitudinal stripes, and lightly tinted wing pattern. *Chrysops atlanticus* inhabits the Atlantic coast from Maine to Florida while *C. sandyi* is found along the Gulf coast of Alabama, Mississippi, and Louisiana.

Variation in *C. sandyi* occurs in the ground color of the mesoscutum, and in the abdominal pattern. Ground color of the mesoscutum, although usually greenish iridescent, may have yellow tomentum. Abdominal pattern may be indistinct, with a pattern of black hair and no integumental markings.

Specimens with these features appear similar to *C. flavidus,* but *C. sandyi* is smaller, wing tinted in the usual hyaline areas, and flagellum subequal to the combined length of the scape and pedicel.

Chrysops tumidicornis Baier, new species

(Figs. 11, 21, 29)

Diagnosis.—Black and brown, length 5.8–8 mm. Antenna swollen, pedicel barrel shaped. Frontal callus width approximately 2 times height. Mesoscutum grey green with black stripes. Wing with distinct hyaline triangle, cells br and bm ⅔ and ¼ infuscated basally.

Holotype female.—Length 7.4 mm. Scape and pedicel swollen, pedicel barrel shaped, brown, covered with black setae, basal flagellomere brown, apical 4 flagellomeres black, flagellum subequal to length of scape and pedicel combined, basal flagellomere equal to combined length of the apical 4 flagellomeres, antennal ratio 14:11:26. Frontoclypeus glossy yellow, eye margins bearing yellow tomentum that extends medianly beneath tentorial pits to frontoclypeal suture. Maxillary palp light brown with scattered stiff black hairs, length 4 times width of apical palpomere. Frons yellow tomentose, slightly convergent above, height 1.2 times width at base. Frontal callus oval, slightly bulbous, yellow, width 1.9 times height. Vertex yellow brown except glossy black around each ocellus, ocelli black. Mesoscutum grayish-green ground color with 3 longitudinal black stripes not merging basally, median one narrower than two sublaterals, yellow tomentose above wing bases. Scutellum black basally, reddish brown apically. Fore coxa, femur and basal ⅓ of tibia yellow, remaining tibia brown, black setose, tarsus entirely dark brown, black setae, mid coxa brown, femur, tibia and basal tarsomeres yellow, tarsi and apical ¼ of tibia with black setae, hind coxa, femur and tibia brown, scattered yellow hair and black setae, black setae becoming more dense toward apical portion of tibia and tarsus. Wing pattern distinct, apical spot includes apical ¾ of vein R_4, reaching posterior half of 2nd submarginal cell, and fading along hind margin of wing to crossband, hyaline triangle slightly tinted, not reaching vein R_{2+3}, outer margin of crossband straight, 5th posterior cell infuscated along margins, center hyaline, cells br and bm ⅔ and ¼ infuscated basally respectively. Abdominal tergites orange yellow, 1st tergite dark brown under scutellum, tergite 2 with median black inverted "V" pattern on integument not reaching anterior, posterior or lateral margins, scattered black hair over dark pattern, median orange triangle behind inverted "V" pattern, hind margin gray, tergite 3 with gray posterior border widened medianly to form an indistinct triangle, anterior half with black pattern of 2 half circles that merge above triangle and occupy ⅓ width of tergite, tergites 4–6 black anteriorly, posterior border gray. Abdomen orange yellow ventrally, sternites 3–5 with median dark spot becoming wider on each successive sternite, sternites 6–7 dark brown.

Male.—Unknown.

Material examined.—Holotype ♀, FLORIDA: Levy County, Cedar Key Shell Mound, VII-7-1976, R. H. Roberts (FSCA). Paratypes: 206 ♀. FLORIDA: Bay County, 2 ♀ V-14-1957, F. W. Mead (CASC); 1 ♀ V-25-1982, J. Hogsette (FSCA); Saint Andrews St. Park, 1 ♀ V-14-1957, F. W. Mead (CASC). Citrus County, 3 ♀ Ozello, VII-29-1959, H. V. Weems (CASC). Collier County, 1 ♀ Collier-Seminole State Park, XI-26-1976, John Edward Rawlins (CUIC). Dade County, 1 ♀ Everglades National Park, I-29-1959, H. A. Denmark (CASC); 1 ♀ Royal Palm Hammock, VI-22-1951, Price, Beamer & Wood (CASC); 1 ♀ West Lake, XII-4-1970, P. H. & M. Arnaud (CASC). Dixie County, 2 ♀ Jena, VII-27-1991, Jena, 10 mi S on RT 361, VII-22-1985 (2 ♀), VII-13-1991 (8 ♀), VII-21-1991 (5 ♀), VII-27-1991 (4 ♀), VIII-31-1991 (13 ♀), VII-11-1992 (1 ♀) L. R. Davis, Jr. (FSCA); 3 ♀ Suwannee, V-19-1964,

C. F. Zeiger (CASC); 2 ♀ Suwannee, V-19-1964 (FSCA). Franklin County, Carrabelle, IV-25-1980 (2 ♀), IV-27-1980 (3 ♀), IV-28-1980 (1 ♀), IV-29-1980 (4 ♀), V-4-1980 (5 ♀), IV-14-1977 (1 ♀), L. L. Pechuman (CUIC); IV-28-1980 (1 ♀), V-4-1980 (1 ♀), L. L. Pechuman (FSCA); Eastpoint, 1 ♀ V-19-1935 (FSCA); Lake Morality, IV-27-1980 (1 ♀), V-10-1980 (1 ♀), 1 ♀ Timber Island, V-4-1980, L. L. Pechuman (CUIC); 1 ♀ Timber Island, V-4-1980, L. L. Pechuman (CASC); 2 ♀ St. George Island, IV-5-1976, L. L. Pechuman (FSCA). Gilchrist County, 1 ♀ VI-2–1950, (CASC). Gulf County, 4 ♀ V-11-1973, J. T. Goodwin (FSCA), V-4-1973 (1 ♀), VIII-14-1971 (1 ♀), H. V. Weems, Jr (FSCA). 2 ♀ St. Joseph State Park, V-1/3-1970, W. W. Wirth (USNM); 1 ♀ V-5-1987, L. Strange and J. Wiley (FSCA). Hernando County, 1 ♀ Bayport, IV-22-1978, L. A. Strange (FSCA). Hillsborough County, 1 ♀ Tampa, IV-29-1950, G. B. Worth (CASC). Jefferson County, 1 ♀ Monticello, IX-18-1935, G. B. Fairchild (FSCA). Lee County, 2 ♀ Sanibel Island, IV-8-1933, W. J. Clench (USNM); 2 ♀ Sanibel Island IV-8-1933, W. J. Clench (FSCA). Levy County, 2 ♀ VII-8-1980, E. Davis (FSCA); 1 ♀ V-6-1955, H. V. Weems (FSCA); 3 ♀ Cedar Key VI-20-1974, (FSCA); 5 ♀ Cedar Key area, VI-4-1991, J. Huether (CUIC); 3 ♀ Cedar Key, VII-12-1939, R. H. Beamer (CASC); 3 ♀ VI-12-1939, Oman (USNM); 1 ♀ VII-29-1977, L. R. Davis, Jr. (FSCA); 1 ♀ VI-28-1973, Carl Shleck (FSCA); 1 ♀ VI-15-1979, L. A. Wood (FSCA); Cedar Key, Shell Mound, VI-9-1971 (5 ♀), VI-16-1973 (1 ♀), VI-29-1976 (6 ♀), VII-3-1976 (7 ♀), G. B. Fairchild (FSCA); 1 ♀ 3 mile E. Shell Mound, 2 ♀ VI-9-1971, (FSCA); 8 ♀ VII-7-1976, R. Roberts (FSCA); 3 ♀ VI-21-1973, R. Wilkerson (FSCA); Yankeetown, V-8/13-1980 (1 ♀), VII-8-1980 (1 ♀), V-16-1980 (3 ♀), VI-24-1980 (5 ♀), E. Davis (FSCA); V-21/23-1979 (1 ♀), V-14/16-1979 (2 ♀), V-11/14-1979 (1 ♀), V-23/24-1979 (3 ♀), V-25/30-1979 (2 ♀), V-30/31-1979 (1 ♀), Roberts (FSCA); 3 ♀ V-30/31-1985, D. L. Kline (FSCA); VIII-10-1966 (1 ♀), VII-28-1965 (4 ♀), C. F. Zeiger (FSCA). Manatee County, 1 ♀ VI-12-1925, T. H. Hubbell (CASC). Monroe County, 1 ♀ Everglades National Park, IV-8-1970, W. W. Wirth (USNM). Okaloosa County, 4 ♀ V-12-1972, J. T. Goodwin (FSCA). Pasco County, 5 ♀ Hudson, VII-13-1939, R. H. Beamer (CASC); 11 ♀ VII-13-1939, Oman (USNM); 1 ♀ VII-13-1939, Oman (FSCA); 2 ♀ VII-13–1939, D. E. Hardy (CASC): Pinellas County, 1 ♀ IV-19-1930, B. P. Moora (USNM); 1 ♀ V-2-1955, R. P. Essar (FSCA); 1 ♀ V-10-1955, E. W. Holder, Jr. (FSCA); 1 ♀ Dunedin, V-14-1959, O. L. Cartwright (USNM); 2 ♀ Pass-a-grille, IV-7-1930, W. G. Fargo (CASC). Santa Rosa County, 1 ♀ Santa Rosa Island, V-24-1971, H. V. Weems Jr. (FSCA); Taylor County, 1 ♀ Steinhatchee, VII-12-1966, R. P. Esser (CASC); 1 ♀ Steinhatchee, VII-20-1991, L. R. Davis, Jr. (FSCA); 1 ♀ 12 mi NW of Steinhatchee, V-24-1983, R. M. Reeves (UNHC); 12 ♀ Cedar Island, 16 miles NW of Steinhatchee, V-16-1969, H. V. Weems, Jr. (FSCA); 3 ♀ Cedar Island, 16 miles NW of Steinhatchee, V-16-1969, H. V. Weems, Jr. (CASC). Wakulla County, 1 ♀ V-2-1980, L. L. Pechuman (CUIC); 3 ♀ Ochlockonee River State Park, V-20-1968, H. V. Weems, Jr. (FSCA); 2 ♀ Ochlockonee River State Park, V-20-1968, H. V. Weems, Jr. (CASC); 1 ♀ Ochlockonee River State Park, VI-22-1973, Fairchild & Wilkerson (FSCA).

Etymology.—This species is named for its characteristic "robust" pedicel.

Distribution.—West coast of Florida.

Biology.—Based of the collection data, most adults have been taken between April–August with a few collected in September, and November–January. All specimens examined were taken from coastal counties near brackish habitats. Although the larva and pupa are unknown, I suspect this species is limited to salt marshes.

Discussion.—This species has been confused with *C. atlanticus* because they both have swollen antennae. Also, I believe that

Pechuman (1949), in his description of *C. atlanticus,* had before him specimens of this species. He wrote that many specimens examined showed considerable melanism, varying from slight enlargement of abdominal spots to extreme enlargement where the tergites were mostly dark with a narrow yellow-brown margin, a pattern I find to be diagnostic *C. tumidicornis.*

In the commonly used keys to species of North American *Chrysops* (Jones and Anthony 1964, Teskey 1969, Tidwell 1973, Pechuman 1973, 1981) *C. tumidicornis* will key to *C. atlanticus.* However, *C. tumidicornis* differs by having a stouter pedicel, frontal callus approximately twice as wide as tall, wing pattern with a distinct hyaline triangle, and an abdominal pattern brown with median orange triangles. *Chrysops tumidicornis* has an extensive apical spot reaching posterior half of 2nd submarginal cell, and a hyaline triangle that does not reach vein R_{2+3}. *Chrysops tumidicornis* appears to be more similar to *C. pudicus* in size, dark mesoscutum and abdominal pattern.

Variation within *C. tumidicornis* ranges from specimes with small, slender body, and a more uniformly dark abdomen, to a larger, more robust body, with an abdominal pattern more uniformly yellow-orange. Three specimens from Gulf County, Florida, have an entirely dark brown abdomen with a lighter median triangle on the 2nd tergite. *Chrysops tumidicornis* is easily recognized by its bulbous, barrel shaped pedicel.

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TWO NEW SPECIES OF *PHAENOCARPA* FOERSTER (HYMENOPTERA: BRACONIDAE: ALYSIINAE) FROM SOUTH AMERICA

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Abstract.—Two **new species** of *Phaenocarpa* Foerster are described from South America: ***P. hyalina* Trostle** and ***P. pericarpa* Wharton and Carrejo**. *Phaenocarpa pericarpa* was reared from *Anastrepha distincta* Greene in pods of *Inga,* representing the first host record for *Phaenocarpa* in South America. A key separating the South American species of *Phaenocarpa* is included.

Key Words: *Anastrepha*; parasitoid; Diptera; Neotropical

Papp (1969) revised the species of *Phaenocarpa* Foerster for the Neotropical Region, treating 10 species. Papp (1966, 1969) included *Asobara* Foerster as a synonym of *Phaenocarpa* in his earlier works, but Fischer (1971) subsequently removed *Asobara* from synonymy and it has been recognized as a separate genus ever since. Consequently, five of the 10 species treated by Papp (1969) must now be placed in *Asobara.* These are *anastrephae* (Muesebeck), *gahani* (Papp), *mexicana* (Ashmead), *pleuralis* (Ashmead), and *rubra* (Papp). Their identity has been confirmed by one of us (RAW), and the placement of two of these species has been discussed previously (Wharton 1994).

A sixth species, *delicata* Papp, has several unusual features, and its placement is uncertain (Wharton 1980, Fischer 1994). Papp (1969) divided the four remaining species into those with well-developed notauli and those without. Wharton (1994) described three additional species from the Neotropics. He further defined two distinct species groups to accomodate these, and discussed the differences which set these two groups apart from other described species of *Phaenocarpa.*

Two more species are described here. The first belongs to the *cratomorpha* Wharton species group as defined by Wharton (1994). The second belongs to Papp's (1969) group with reduced notauli.

The genus *Phaenocarpa* is fairly large, but hosts have been recorded for only about 15% of the 150 described species (Fischer 1974, 1975, 1990, 1993; Shenefelt 1974; Wharton 1984; Vet and van Alphen 1985; Tobias 1986). Holarctic species have been reared most frequently from calypterate Diptera breeding in such habitats as fungus, dung, flower heads and other seed bearing structures. A few have also been recorded from acalypterates such as drosophilids and sciomyzids (Papp 1972, Fischer 1975, Wharton 1984, Vet and van Alphen 1985, van Achterberg 1988). Hosts have not been previously recorded for any of the Neotropical species of *Phaenocarpa.*

Materials and Methods

Terminology is as in Wharton (1980, 1994) except as follows: venation conforms

to the standards recently established by Sharkey and Wharton (1997); scutellar sulcus is used in place of prescutellar pits; the terms mesonotal disc (or simply disc) and anterior declivity are retained in their former meaning, but are referred to as parts of the mesoscutum. Measurements are given to the nearest 0.05.

Museum acronyms are as follows: The Natural History Museum, London (BMNH), Texas A&M University Insect Collection (TAMU). Part of the material for this study was sorted from general BMNH accessions by RAW, the remainder was reared by NSC as part of a program to determine natural enemies of fruit-infesting tephritid flies of the genus *Anastrepha* in Colombia.

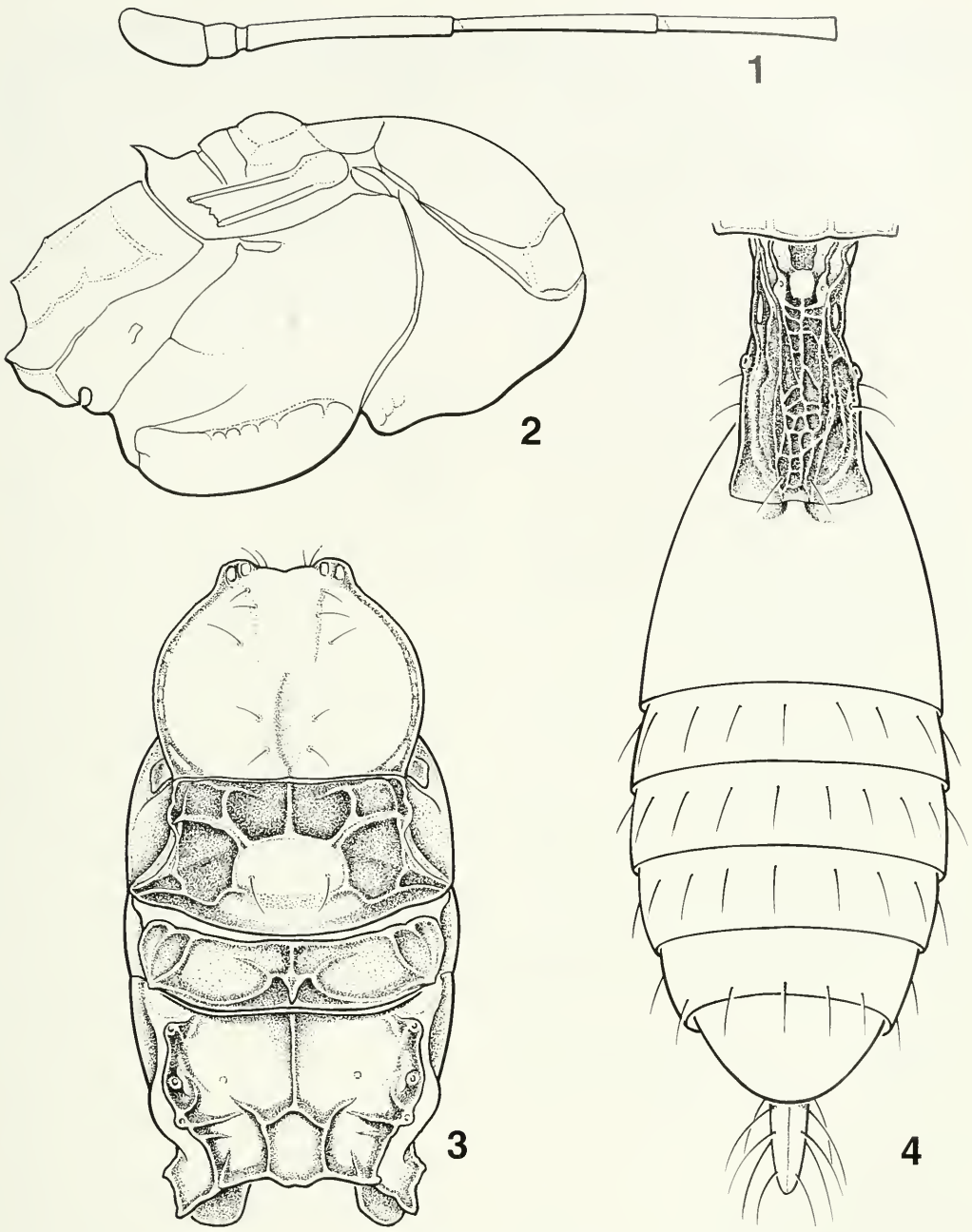
Key to Neotropical Species of *Phaenocarpa*

1. Second flagellomere at least 1.4 times longer than first (Figs. 12–14) 2
– Second flagellomere at most 1.1 times longer than first (Fig. 1) 6
2. Second submarginal cell short, with 2RS nearly equal to or slightly longer than 3RSa 3
– Second submarginal cell longer (Fig. 7), with 3RSa at least 1.25 times longer than 2RS . . . 4
3. Notauli distinct posteriorly. Mandible with tooth 1 extending distinctly distad tooth 3 . . . . . *Phaenocarpa coxalis* (Szépligeti)
– Notauli absent posteriorly, not reaching midpit on mesoscutum. Mandible with tooth 3 extending distinctly distad tooth 1 . . . . . *Phaenocarpa anomala* Wharton
4. Mandible with broad tooth 1 separated from tooth 2 by a deep cleft (Fig. 15). Fore wing (RS+M)b distinctly more than half length of m-cu (Fig. 7) . . . . . *Phaenocarpa pericarpa* Wharton and Carrejo, n. sp.
– Mandibular teeth 1 and 2 connected by a broad, undulant flange, not separated from each other by a deep cleft (Fig. 10). Fore wing (RS+M)b short to absent, distinctly shorter than half length of m-cu 5
5. Petiole dark brown, narrowly elongate, about 1.5 times longer than apical width; apex about 1.6 times wider than base. Propodeal areola distinct; transverse carina of propodeum absent laterally . . . . . *Phaenocarpa heynei* Papp
– Petiole dark yellow, broader, about 1.2 times longer than apical width, apex about twice wider than base. Propodeal areola indistinct; transverse carina complete to spiracles . . . . . *Phaenocarpa subtilistriata* Papp
6. Stigma of fore wing broad distally, abruptly narrowing basad junction with r in females (Fig. 5), with posterior margin indistinct on basal half; divided by a hyaline, desclerotized line in males, with portion of stigma posteriad hyaline region broader than portion along anterior margin of wing (Fig. 6). Mesopleuron, metapleuron, and propodeum dark brown. Metanotum in lateral view with short but distinct spine (Fig. 2) . . . . . *Phaenocarpa hyalina* Trostle, n. sp.
– Stigma of fore wing narrow distally and basally, only gradually narrowing basad junction with r in females, with posterior margin clearly delineated on basal half; males in which the stigma is divided by a desclerotized line have the portion that is posteriorad the desclerotized, hyaline region narrower than the portion along the anterior margin of the wing. Body color and development of metanotal projection variable 7
7. Mesopleuron, metapleuron, and propodeum yellow. Metanotum in lateral view with short, narrow spine-like projection (as in Fig. 2) . . . . . *Phaenocarpa sharkeyi* Wharton
– Mesopleuron, metapleuron, and propodeum dark brown, contrasting with light brown to yellow mesoscutum. Metanotum in lateral view with broadly triangular projection (distinctly broader than high) . . . . . *Phaenocarpa cratomorpha* Wharton

Phaenocarpa hyalina Trostle, new species

(Figs. 1–6)

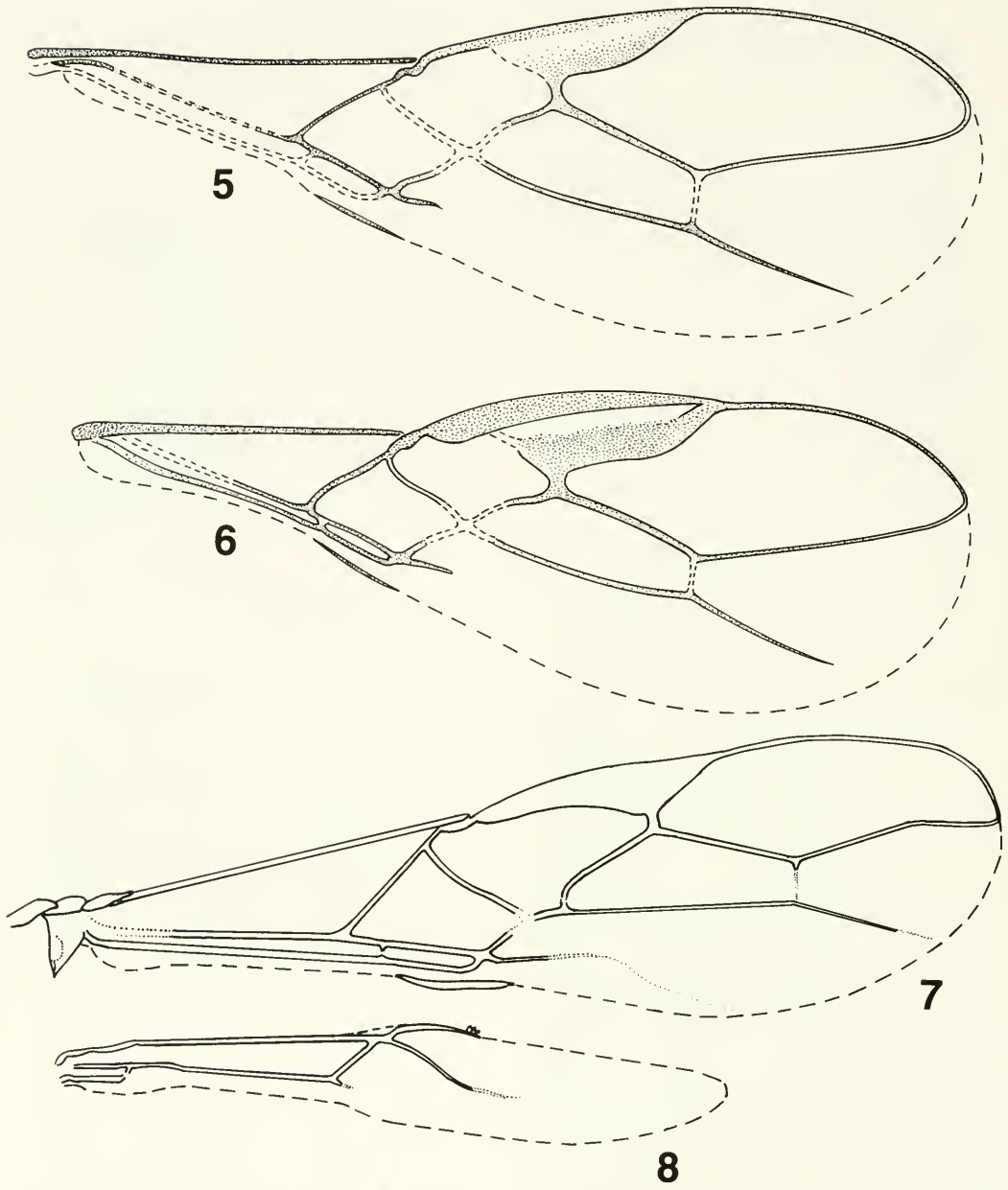
Female.—*Head:* Moderately transverse in dorsal view, 1.3× wider than long. Face punctate, setiferous but polished, 1.25–1.35 higher than wide. Frontoclypeal suture broad, relatively shallow, unsculptured. Clypeus broad, weakly convex, barely protruding. Frons smooth, bare, nearly flat, weakly concave medially. Mandible 1.85× longer than width between tooth 1 and 3, surface largely smooth; tooth 1 broad, nearly orthogonal, with dorsal margin concave; distinct cleft present between tooth 1 and 2, tooth 2 lacking additional tooth or knob; tooth 2 acutely triangular, short, 0.4–0.45× apical width of mandible, but extending beyond tooth 1 and 3; tooth 3 broadly trian-



Figs. 1–4. *Phaenocarpa hyalina*. 1, Antenna showing relative lengths of basal 3 flagellomeres. 2, Mesosoma, lateral view, showing metanotal spine. 3, Mesosoma, dorsal view. 4, Metasoma, dorsal view.

gular. Eye large, 4.25–5× longer than temple. Anterior tentorial pit large, extending more than 0.5× distance from lateral margin of clypeus to eye. Antenna 25–27 segmented; second flagellomere 1.0–1.05× longer than first; first flagellomere 1.1–1.3× longer than third. Eye-antennal sulcus absent.

Mesosoma: 1.35–1.5× longer than high. Pronotum predominately smooth, with lon-



Figs. 5–8. Wings. 5, *Phaenocarpa hyalina*, female. 6, *P. hyalina*, male. 7, 8, *P. pericarpa* fore and hind wing.

gitudinal carina separating dorsal and lateral portions, and fine crenulae laterally extending ventrally from this carina; pronotum dorsally a narrow band with a shallow, barely perceptible median pit; anterior margin weakly emarginate. Mesoscutum polished; anterior declivity vertical, sparsely setose; notauli extending medially as carinate ridges along dorsal margin of anterior declivity, then proceeding posteriorly as weak, parallel grooves perpendicular to the carinate ridges, notaular grooves evanescent

near anterior margin of midpit; 3–4 pairs of setae extending from transverse portion of notauli to transscutal articulation; midpit well developed, extending anteriorly 0.4× length of disc from transscutal articulation. Scutellar sulcus about 2× broader than long, with medial carina; lateral margins of axilla flangelike. Metanotum with posterior margin a broad, flat plate, elevated medially as a prominent spine, median field with or without carinae radiating from spine. Propodeum areolate, as in other members of the *cratomorpha* species group. Mesopleuron with small patch of rugose sculpture on anterior margin medially, otherwise smooth, polished, virtually bare; carinately margined posteriorly. Sternaulus sinuate, crenulate over anterior 0.65, smooth over posterior 0.35. Metapleuron largely unsculptured, as in *P. sharkeyi*.

Wings: Fore wing stigma 4.5–5.0× longer than broad, solid throughout (i.e., without hyaline streak), basal half distinctly narrower than distal half with posterior margin of basal half indistinct and somewhat excavated, stigma abruptly widening near junction with r; r short, slightly shorter than and arising slightly distad mid-width of stigma; 3RSa 1.4–1.8× longer than 2RS; 3RSb extending to wing tip, weakly curved at apex; (RS+M)b usually absent; 1cu-a often very short, postfurcal by 1.25–3.5× its length. Hind wing with 1M 2.4–3.5× longer than M+CU; 3 hamuli.

Metasoma: Petiole 1.6–1.7× longer than apical width, apex 1.5–1.6× wider than base, dorsal carinae on petiole more or less parallel sided, weakly converging and becoming less prominent posteriorly; surface sculpture often granular-rugose medially; more finely rugose laterally. Ovipositor sheath with 3 irregular rows of approximately 7 setae each. Ovipositor 0.9× and ovipositer sheath 0.65× length of mesosoma.

Color: Generally brown; mesoscutum, metanotum and occasionally propleuron bright orange yellow; mesopleuron, metapleuron, propodeum and petiole dark brown; legs white at coxae and gradually darkening to yellow distally; maxillary palp white; face variable, dark brown to light orange yellow, usually paler near antennae; scape and pedicel bright yellow with pedicel slightly paler; basal 16–18 flagellomeres gradually darkening from yellow to brown distally, followed by 4–7 white flagellomeres, and terminating with 1–3 (usually 1.5) brown flagellomeres; wings hyaline.

Body length: 2.1–2.4 mm

Male.—Similar to female except as follows: head 1.3–1.4× wider than long; face 1.1–1.2× higher than wide; mesosoma 1.45–1.55× higher than wide; body 2.3–2.9 mm; fore wing stigma longitudinally bisected for most of its length with the thickened portion along anterior margin of wing almost completely separated from posterior portion by hyaline streak, the two portions only narrowly joined distally, posterior portion broader than anterior portion.

Biology.—Unknown

Material examined.—Holotype ♀: "Brasilien Nova Teutonia 27°11′B. 52°23′L. 2-ix-1935 Fritz Plaumann" (BMNH). Paratypes (BMNH, TAMU): 2 ♂, same data as holotype; 2 ♀, 10 ♂, same except viii.1935, xi.1935, 6.iii.1936, and 15.x.1935; 1 ♀, 2 ♂, same locality but country spelled "Brazil:" and with B.M Accession label "B.M.1937-656", collected 11.vii.1937, and 7.v.1937; 2 ♀, 2 ♂, same as preceding, but "B.M. 1938-682", collected 20.iv.1938, 13.viii.1938, 23.iv.1938, and 3.v.1938.

Diagnosis.—This species is a member of the *cratomorpha* species group as defined by Wharton (1994). As in other species of this group, *P. hyalina* has the second flagellomere equal to or barely longer than the first (Fig. 1), a median metanotal projection (Fig. 2), and a hyaline streak longitudinally bisecting the male stigma (Fig. 6). The stigma is sexually dimorphic, lacking a well-defined streak in females. *Phaenocarpa hyalina* differs from other described species of this group in the possession of a broader stigma that narrows more abruptly basad

the junction with r. Further, the metanotal projection of *P. hyalina* is much more spinose than in *P. cratomorpha,* displaying a thinner, finer apex. Obvious color differences exist between *P. sharkeyi* and *P. hyalina. Phaenocarpa sharkeyi* is more uniformly pale yellow in coloration, contrasting with the darker brown portions of the head, meso- and metasoma of *P. hyalina.*

Discussion.—This species is named for the hyaline streak that almost completely bisects the stigma in males, resulting in separate anterior and posterior portions. Additional differences in size and shape between males and females were noted by Wharton (1994) in his description of *P. cratomorpha.* Detailed scrutiny of males and females of *P. hyalina,* however, fails to reveal significant differences between the sexes for most of these same characters. Since so few individuals of *P. cratomorpha* were available for study, it is quite possible that the differences recorded by Wharton (1994) in the size and shape of the eye and petiole were simply intraspecific rather than specifically intersexual. Measurements of individuals from the much longer series of *P. hyalina* demonstrate that these quantitative characters are highly variable within each sex.

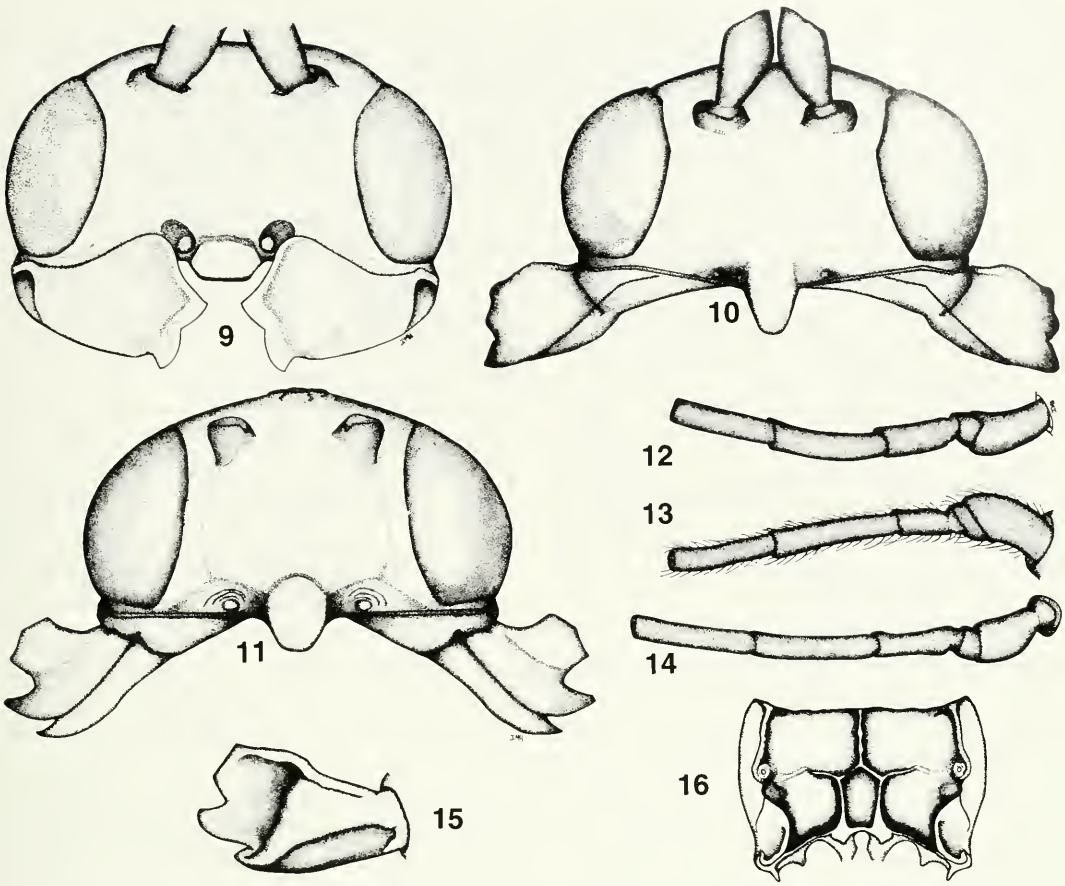
Although a distinct hyaline streak is present in males and absent in females, the stigma in females of *P. hyalina* exhibits modifications suggesting a morphocline leading to the extreme condition expressed in males. The stigma in females has a slight indication of desclerotization in a position comparable to the basal portion of the hyaline streak in males. Further, the stigma is exceptionally narrow basally, distad the parastigma, then somewhat abruptly widens where it meets r. In most other species of *Phaenocarpa,* the posterior margin of the stigma is straight to evenly convex between r and the parastigma. *Phaenocarpa hyalina* and the species described below are exceptional in this regard.

Phaenocarpa pericarpa Wharton and Carrejo, new species

(Figs. 7, 8, 11, 14–16, 19)

Female.—*Head:* Moderately transverse in dorsal view, about 1.5–1.6× wider than long; eyes strongly bulging beyond temples. Face finely punctate, the punctations separated by much more than their diameter, otherwise smooth and polished between base of antenna and frontoclypeal suture; frontoclypeal suture deep and very wide, transversely striate; clypeus exceptionally narrow and strongly protruding, lateral margin of clypeus distinctly separated from anterior tentorial pit, the latter small, set within broad concavity between clypeus and lower margin of eye, the concavity transversely striate at least in part. Malar space absent. Frons smooth, polished, evenly and weakly convex, bare except for 2–4 short setae along eye margin laterad ocelli. Vertex bare. Mandible 1.4–1.5× longer than apical width, distinctly expanded apically, apex 1.7–1.85× wider than base, surface with strigose sculpture extending from middle of diagonal ridge to dorsal margin at base of tooth 1; tooth 1 very broad, orthogonal, separated by deep cleft from narrowly triangular tooth 2; tooth 2 without dorsal knob; tooth 3 extending distally not quite as far as tooth 1, narrower and more rounded than the latter. Eye very large, 5.2–6.0× longer than temple, with a few, scattered, minute setae visible at 50×. Antenna 39 segmented; second flagellomere 1.5–1.7× longer than first, 1.1× longer than third. Maxillary palp very long, about twice height of head.

Mesosoma: 1.45–1.55× longer than high. Pronotum dorsally smooth, polished, but uneven: with small, u-shaped depression medially along anterior margin; weakly elevated as a small, rounded bump posteromedially; flattened laterally. Mesoscutum smooth, polished, with setae confined to a short row along notauli on anterior declivity, absent on disc; notauli shallow, weakly sculptured, confined to anterior de-



Figs. 9–16. *Phaenocarpa* spp. 9–11, Faces. 9, *P. subtilistriata.* 10, *P. heynei.* 11, *P. pericarpa.* 12–14, Antennae showing relative lengths of basal 3 flagellomeres (setal pattern shown only on Fig. 13). 12, *P. subtilistriata.* 13, *P. heynei.* 14, *P. pericarpa.* 15, *P. pericarpa,* mandible. 16, *P. pericarpa,* propodeum.

clivity; midpit small, shallow, oval. Scutellar sulcus twice as wide as long, or nearly so; with a single median ridge; lateral fields polished, unsculptured. Metanotum with thin, longitudinal flange along midline, the flange sloping more precipitously anteriorly than posteriorly, not elevated above level of scutellum. Propodeum smooth, polished, with well-defined pentagonal areola delimited by strong carinae; areola narrow, about half as wide as tall, confined to posterior half of propodeum; anterior half with a strong median carina; lateral carina extending from areola to spiracle usually very weak over lateral half. Sternaulus long, narrow, sinuate, complete from anterior margin to mid coxa, weaker posteriorly; crenulate anteriorly, the sculpture weakening posteriorly and usually absent over posterior 0.3–0.5. Metapleuron finely punctate but otherwise polished and unsculptured over most of surface.

Wings: Fore wing stigma weakly concave basally along posterior margin, gradually widening distally towards junction with r, solid throughout, about 5× longer than width at r, r arising from distal 0.7–0.75; r very short, 0.15–0.20× length of 2RS; 2RS sharply angled near posterior 0.2; 3RSa 1.25–1.35× longer than 2RS, second submarginal cell gradually narrowing distally; 3RSb ending at wing tip, weakly and evenly bowed; m-cu distinctly antefurcal, with (RS+M)b 0.65–0.8× length of m-cu;

1cu-a postfurcal by 2–3× its length; 2CU interstitial: arising directly in line with 1CU. Hind wing very narrow, about 6× longer than wide; 1M 2.0–2.5× longer than M+CU; 2M very short, angled towards posterior margin, m-cu absent.

Metasoma: Petiole 1.3–1.45× longer than apical width; apex 1.8–1.9× wider than base; surface strigose, the sculpture distinct medially, often weak laterally; dorsal carina strong basally, evanescent at level of spiracles, absent posteriorly; dorsope large and deep. Remaining terga without sculpture. Ovipositor of moderate length, ovipositor sheath not fully exposed in material available for examination, but about 2.0–2.3× longer than mesosoma; ovipositor finely tapered to apex, without discernible subapical node or notch.

Color: Dark brown; mandible, scape, pedicel, propleuron and petiole variously lighter brown or red-brown in most specimens; flagellomeres 1–4 brown, 5–12 and 19–29 dark brown, 14–18 white, and 13 bicolored brown and dark brown; fore and mid legs and hind coxa and trochanter yellow to dark yellow, hind femur mostly yellow with dark spot dorsally over apical 0.3–0.4, hind tibia and tarsus brown; hypopygium apically and apical tergite yellow or yellow brown; palps white.

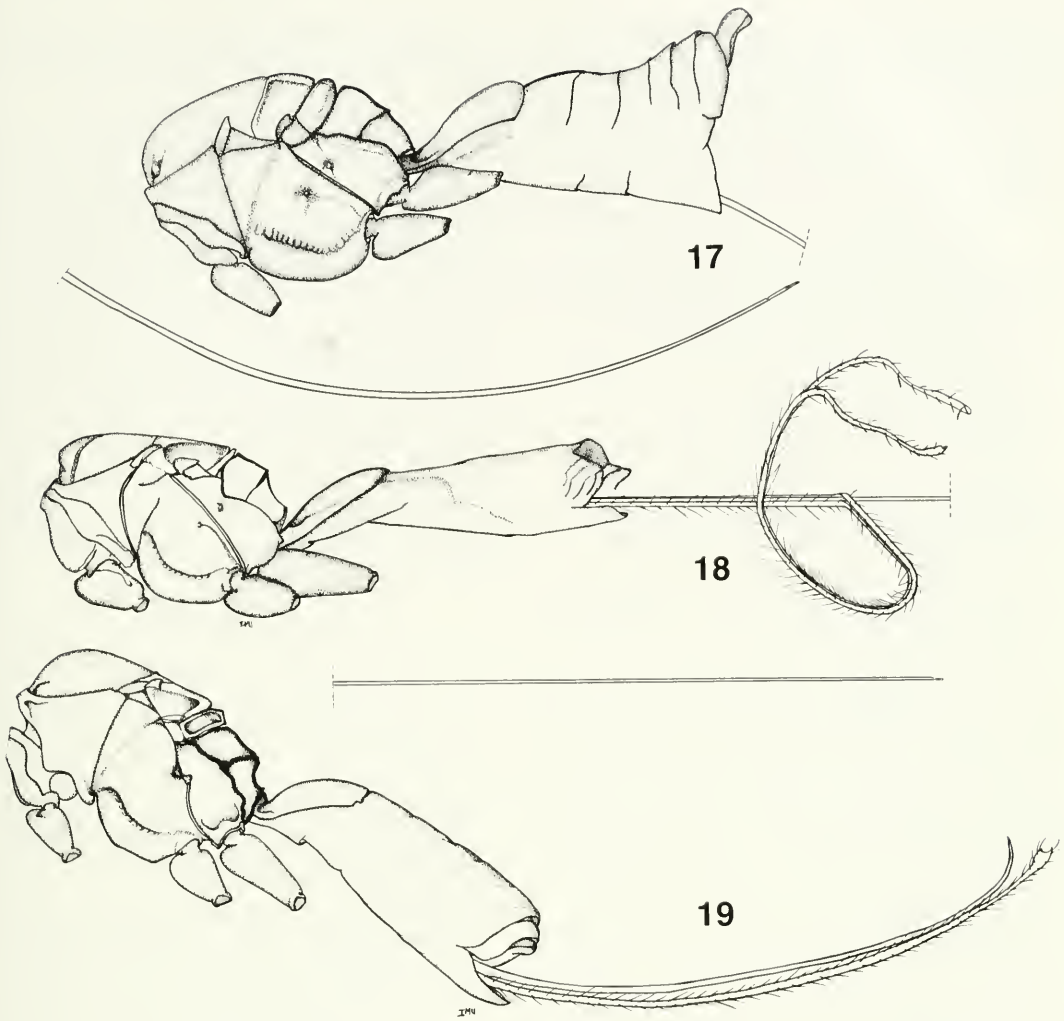
Male.—A single male, probably representing this species, fits the above description except as follows: face shorter, about 1.5× wider than high; mandible less expanded distally, about 1.8× longer than apical width; fore wing 1cu-a postfurcal by only about 1.4× its length; and fore wing 3RSa about 1.6× 2RS. Flagellomeres 15 and 16 are dirty white, with remaining flagellomeres dark brown.

Biology.—Reared from puparia of *Anastrepha distincta* Greene in pods of guama (*Inga* sp.: Fabaceae).

Material examined.—Holotype ♀: "COLOMBIA Dept. del Valle del Cauca Mun. Buenaventura, Corregimiento de Zacarias 23.iii.1994 N. Carrejo ex Anastrepha distincta on Guama" Deposited in La Universidad del Valle, Museo de Entomología. *Paratypes:* 3 ♀, same data as holotype (TAMU; Universidad del Valle; and Instituto de Ciencias Naturales, Universidad Nacional de Colombia). *Additional material (not a paratype):* 1 ♂, VENEZUELA, Aragua, Parque Nacional Henri Pittier, Rancho Grande, 1,100m, 12.i.1996, R. Wharton (TAMU).

Diagnosis.—As in both *P. heynei* and *P. subtilistriata,* this species has reduced notauli, a short first flagellomere, and a large second submarginal cell. It differs from both of these species by the possession of a shorter ovipositor (compare Fig. 19 with Figs. 17, 18) which lacks a subapical node or notch and a broader, more discrete tooth 1 on the mandible (Fig. 15). The ovipositor is more than three times longer than the mesosoma in *P. heynei* and *P. subtilistriata.* The shape of the mandible is sufficient for separating *P. pericarpa* from all other described New World species of *Phaenocarpa.*

Discussion.—Papp (1969) adequately differentiated *P. heynei* from *P. subtilistriata,* noting especially the difference in shape of the petiole. There are also slight differences in sculpture between the holotypes of *P. heynei* and *P. subtilistriata.* The propodeal areola is essentially obliterated in *P. subtilistriata,* with the posterior face strigose or weakly rugulose below the well-developed and complete transverse carina. A weak areola is present in *P. heynei,* and the transverse carina is incomplete, not reaching the propodeal spiracle. The sternaulus is also broader and more heavily sculptured in *P. subtilistriata* but the scutellar sulcus is smooth with a single median carina. In *P. heynei,* the scutellar sulcus is weakly sculptured on either side of the median sulcus. Although both *P. heynei* and *P. subtilistriata* are known only from the holotype, and variation thus cannot be assessed, these same sculptural features show little variation in the four specimens of *P. pericarpa.* Thus, it is likely that these relatively minor sculptural differences will be



Figs. 17–19. Meso- and metasoma, lateral view. 17, *Phaenocarpa subtilistriata.* 18, *P. heynei.* 19, *P. pericarpa.*

useful for species-level recognition of *P. heynei* and *P. subtilistriata.*

Several features suggest that *P. heynei* shares a sister group relationship with *P. pericarpa* relative to *P. subtilistriata.* Although the clypeus is narrow in all three species, it is more strongly narrowed and protruding in *P. heynei* and *P. pericarpa* (Figs. 10, 11), with consequent detachment of the anterior tentorial pit from the lateral margin of the clypeus. Similarly, 2M in the hind wing is shorter and more distinctly deflected posteriorly in *P. heynei* and *P. pericarpa* than in *P. subtilistriata,* which retains the more plesiomorphic form of a longer, more distally-directed 2M. The fore wing stigma of *P. heynei* is also more similar to the unusually shaped stigma of *P. pericarpa* than the more typically shaped stigma of *P. subtilistriata. Phaenocarpa subtilistriata* appears to form a link between the *heynei+pericarpa* sister group and the more typical *Phaenocarpa* species from the Holarctic Region. This hypothesized relationship between *P. heynei* and *P. pericarpa* leads the suggestion that the *Gnathopleura*-like mandible of *P. heynei* and *P. subtilistriata* is a more primitive feature from

which the *P. pericarpa* configuration was derived. Despite similarities in the mandible, *P. heynei* and *P. subtilistriata* can be readily separated from *Gnathopleura* since the latter has a much smaller second submarginal cell.

The putative relationship between *P. heynei* and *P. pericarpa* is based on features which, though unusual, are found elsewhere in *Phaenocarpa* and related genera. A similarly narrow hind wing with reduced 2M is found in the *Phaenocarpa cratomorpha* species group, for example. A narrow, strongly protruding clypeus is found in at least two species of *Asobara* (one from Brazil and one from Papua New Guinea) which otherwise lack shared derived features. In all of these cases, the character states in question are hypothesized as independent derivations.

This is the first host record for any of the Neotropical species of *Phaenocarpa.* The type series of *P. pericarpa* was reared from the tephritid fly *Anastrepha distincta* Greene, developing in the pods of guama (*Inga* sp.). Relatively few tephritids have been recorded as hosts of Alysiinae (Wharton 1984). Only one, *Asobara anastrephae* (Muesebeck), has been verified as a parasitoid of fruit-infesting tephritids. *Asobara orientalis* Viereck, originally described from material thought to be reared from dacine tephritids, is undoubtedly a drosophilid parasitoid. Three other alysiine species have been reared either from tephritids in flower heads or other plant parts, and at least four additional species have been reared from unknown hosts in fruit. *Asobara anastrephae* is interesting because of its exceptionally large size and unusual host preferences relative to other species of *Asobara,* which are primarily drosophilid parasitoids. *Asobara anastrephae* belongs to a group of Neotropical species with typical *Asobara* fore wing venation, loss of hind wing cu-a, a short, broad petiole, and brightly colored bodies (Muesebeck 1958, Wharton 1994). One of the derived members of this group, as yet undescribed, exhibits the same clypeal modifications found in *P. pericarpa* and *P. heynei.*

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THE SMALL MINNOW MAYFLY GENUS *CLOEODES* TRAVER (EPHEMEROPTERA: BAETIDAE) IN MADAGASCAR

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Abstract.—***Cloeodes portabilis*, new species**, represents the first report of *Cloeodes* from Madagascar. The species is distinguished in the larval stage by the relatively wide anteromedial emargination of the labrum, presence of tufts of fine, simple setae between the prosthecae and molae of the mandibles, slightly distolaterally acute segment 3 of the labial palps, and abdominal color pattern. The presence of *Cloeodes* throughout the Southern Hemisphere suggests a relatively ancient origin among extant Baetidae.

Key Words: Ephemeroptera, Baetidae, *Cloeodes portabilis,* new species, Madagascar

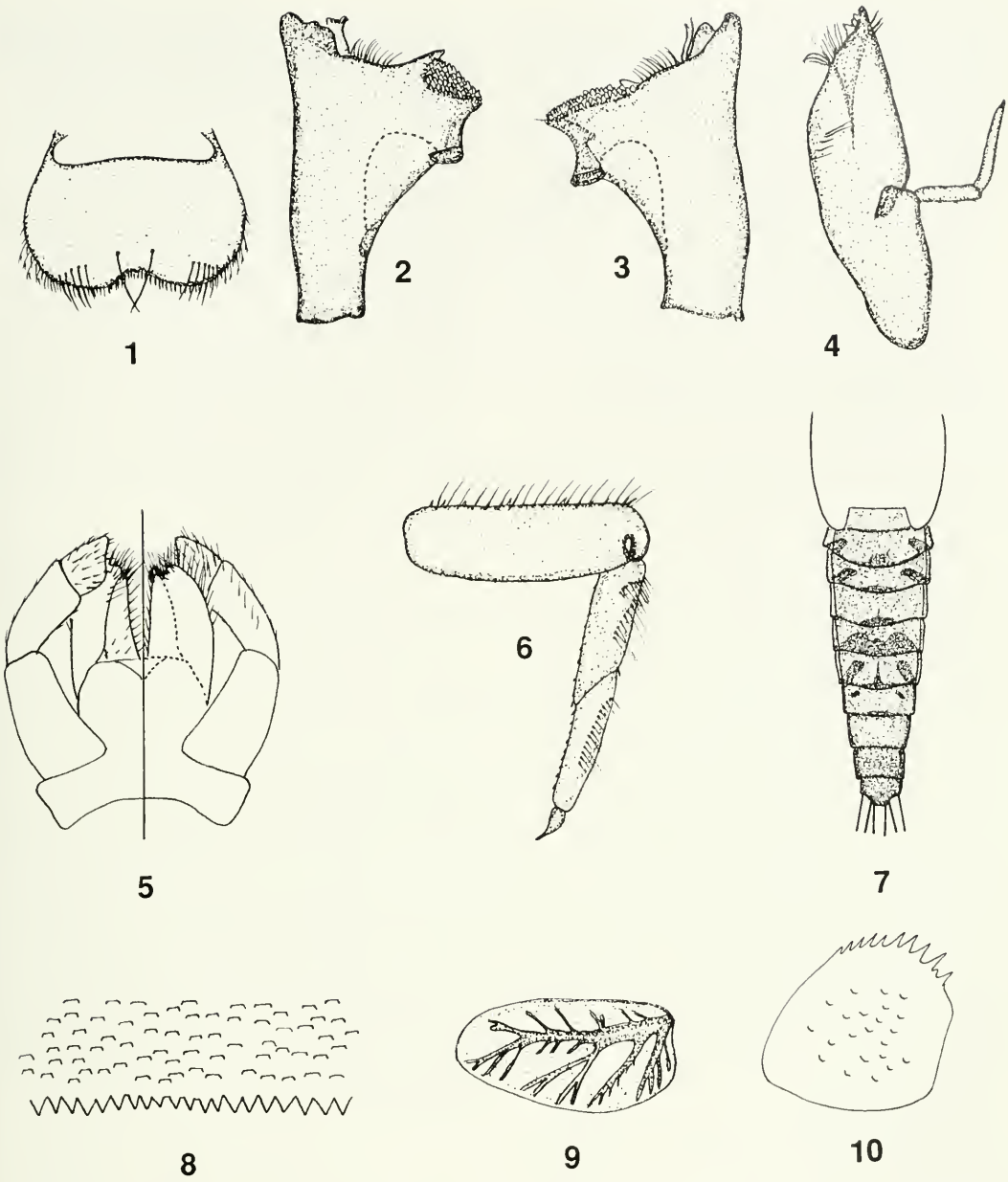
The distinctive small minnow mayfly genus *Cloeodes* Traver (Ephemeroptera: Baetidae) has been known from the Afrotropics, Neotropics, Orient, and southwestern Nearctic (Traver 1938, Waltz and McCafferty 1987ab, 1994, Kluge 1991, Flowers 1991, Lugo-Ortiz and McCafferty 1993, 1994, 1995, McCafferty and Lugo-Ortiz 1995, McCafferty *et al.* 1997). Most recently, Lugo-Ortiz and McCafferty (1998) reported *Cloeodes* from Australia, significantly extending its known range. Three historic biogeographic hypotheses were provided to explain its essentially Pantropical distribution.

That *Cloeodes* was well established throughout Gondwanaland or at least West Gondwanaland (the South American-African-Malagasy-Indian landmass) prior to 100 million years ago, before Madagascar began to separate from Africa and India, were hypotheses that clearly predicted that *Cloeodes* would occur in Madagascar. Herein we report *Cloeodes* from Madagascar for the first time based on a new species described from larvae. An additional species of *Cloeodes* from the island will be described elsewhere by one of us (J.-L.G.). The specimens studied are housed in the Purdue Entomological Research Collection, West Lafayette, Indiana.

Cloeodes portabilis Lugo-Ortiz and McCafferty, new species

(Figs. 1–10)

Larva.—Body length: 3.4–4.4 mm. Caudal filaments length: 1.8–2.0 mm. *Head:* Coloration medium brown, with no distinct pattern. Antenna approximately 1.75× length of head capsule. Labrum (Fig. 1) with wide anteromedial emargination, submedial pair of long, fine, simple setae, and submarginal row of four to six long, fine, simple setae. [Left and right mandibles (Figs. 2, 3) with incisors worn down.] Left mandible (Fig. 2) with one set of incisors; prostheca robust, apically denticulate; tuft of fine, simple setae present between prostheca and mola. Right mandible (Fig. 3) with two sets of incisors; prostheca slender, apically bifid; tuft of fine, simple setae present between prostheca and mola. Maxilla



Figs. 1–10. *Cloeodes portabilis*. 1, Labrum (dorsal). 2, Left mandible. 3, Right mandible. 4, Left maxilla. 5, Labium (left-ventral; right-dorsal). 6, Left foreleg. 7, Abdomen (dorsal). 8, Tergum 3 (detail). 9, Gill 3. 10, Paraproct.

(Fig. 4) with four small, stout denticles on crown of galealacinia; four to five long, fine, simple setae near medial hump; palp not reaching galealacinia; palp segment 1 subequal in length to segment 2; segment 2 apically acute. Labium (Fig. 5) with glossa and paraglossa equal in length; palp segment 1 approximately 0.80× length of segments 2 and 3 combined; segment 2 approximately 1.6× length of segment 3; segment 3 falcate apically and slightly pointed distolaterally. *Thorax:* Coloration yellow

brown, with complex markings. Hindwing-pads absent. Legs (Fig. 6) pale yellow brown; femora dorsally with row of five to six medium-sized, robust, simple setae intermixed with numerous long, fine, simple setae; tibiae ventrally with 10–12 short, stout, simple setae; tarsi ventrally with eight to nine short, stout, simple setae. *Abdomen* (Fig. 7): Coloration medium to yellow brown; segment 1 yellow brown; segment 2 yellow brown, with submedial medium brown subtriangular marking and oblique medium brown distolateral markings; segment 3 with submedial medium brown crescentlike marking posteriorly and oblique medium brown distolateral markings; segment 4 with submedial medium brown crescentlike marking posteriorly; segment 5 with large, wavy, medium brown marking posteriorly; segment 6 with submedial spikelike medium brown marking and oblique medium brown distolateral markings; segment 7 with small, oblong, medium brown anterolateral markings; segment 8 yellow brown, with no markings; segments 9–10 medium brown, with no markings. Terga (Fig. 8) with abundant scale bases, and with posterior marginal spines triangular, approximately as long as basal width. Sterna yellow brown. Gill (Fig. 9) subtriangular, well tracheated, marginally smooth. Paraproct (Fig. 10) with 10–12 spines, increasing in size apically. Caudal filaments pale yellow brown; medial caudal filament subequal in length to cerci.

Adult.—Unknown.

Material examined.—*Holotype:* Larva, MADAGASCAR, Tamatave (= Toamasina) Prov., stream at Gri-Gri, RN 2, 17-X-1971, G. F, C. H. Edmunds, and F. Emmanuel. *Paratypes:* Two larvae, same data as holotype; five larvae, MADAGASCAR, Antsiranana Prov., Djabala R., 11 km NW of Hell-Ville, Nosy Be, 25-X-1971, G. F., C. H. Edmunds, and F. Emmanuel [mouthparts, left foreleg, tergum 3, gills 3, and paraproct of one larva mounted on slide (medium: Euparal)]. *Additional material:* Four larvae, same data as holotype; twenty larvae, MADAGASCAR, Antsiranana Prov., Djabala R., 11 km NW of Hell-Ville, Nosy Be, 25-X-1971, G. F, C. H. Edmunds, and F. Emmanuel.

Etymology.—The specific epithet is a Latin word meaning "that which may be carried." It is an allusion to the species being a drifted representative of the genus.

Discussion.—*Cloeodes portabilis* is distinguished from other members of the genus by the relatively wide anteromedial emargination of the labrum (Fig. 1), presence of tufts of fine, simple setae between the prosthecae and molae of the mandibles (Figs. 2, 3), slightly distolaterally acute segment 3 of the labial palps (Fig. 5), and abdominal color pattern (Fig. 7).

Cloeodes portabilis is unique among Eastern Hemisphere members of the genus because segment 3 of the labial palps is somewhat falcate, being slightly distolaterally pointed (Fig. 5); other species have a bulbous segment 3. Only the South American species *C. hydation* McCafferty and Lugo-Ortiz has a similar labial palp morphology (McCafferty and Lugo-Ortiz 1995: Fig. 6); we can only assume that it constitutes a homoplasy. In addition, the presence of a tuft of setae between the prosthecae and molae of the mandibles in *C. portabilis* (Figs. 2, 3) is exceptional in *Cloeodes*, possibly indicating a relatively ancestral position within the genus, because that characteristic is generally associated with plesiotypic genera in Baetidae (R. D. Waltz, personal communication).

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NEW COMBINATIONS, NEW SYNONYMY, AND HYMONOMY IN THE ERIOCOCCIDAE, NEW HOMONOMY AND SYNONYMY IN THE CEROCOCCIDAE, AND TRANSFER OF *CANCEROCOCCUS* KOTEJA TO THE MARGARODIDAE (HEMIPTERA: COCCOIDEA)

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Abstract.—A database and catalog of the eriococcid and cerococcid scale insects of the world is nearly complete and soon will be in press and placed on the World Wide Web. Before this is done, new combinations and other taxonomic changes need to be validated in print. This publication includes *Neokaweckia* Tang and Hao as a **new synonym** of *Eriococcus*, proposal of ***Neotrichococcus*** as a **new name** for *Trichococcus* Borchsenius, and new combinations in the family Eriococcidae; a new homonym and synonym in the Cerococcidae; and transfer of *Cancerococcus* from Eriococcidae to Margarodidae.

Key Words: felt scales, Coccoidea, Eriococcidae, Cerococcidae, Margarodidae, ScaleNet, catalog, new combinations, Internet

We currently are finishing a database and manuscript on the Eriococcidae and Cerococcidae of the world. This research is part of a larger project called "ScaleNet" to develop a systematic database of the Coccoidea of the World; see Miller and Gimpel (1996), and Ben-Dov et al. (1997). One of the most controversial subjects in synthesizing the systematic data on eriococcids is to make sense out of the genera *Acanthococcus* Signoret, *Anophococcus* Balachowsky, *Eriococcus* Targioni Tozzetti, *Gossyparia* Signoret, *Greenisca* Borchsenius, *Gregoporia* Danzig, *Kaweckia* Koteja and Zak-Ogaza, *Neokaweckia* Tang and Hao, and *Rhizococcus* Signoret. Most European literature recognizes all, or nearly all, of these genera as distinct, e.g., Kosztarab and Kozár (1988), but Hoy (1963) treated many of them as junior synonyms of *Eriococcus* and Williams (1985) treated all but *Gregoporia* as members of *Eriococcus*. *Gregoporia* was first treated as a synonym by Miller and Gimpel (1996) and *Neokaweckia* is here considered as a new junior synonym of *Eriococcus*.

Although some have criticized the lumping of these genera as a reversion to Linnaean times (Koteja 1997), we believe that the characters used to define these genera are homoplasious and discriminate artificial groups. It is logical to assume that natural groups occur in this assemblage, but it is important to undertake a careful phylogenetic analysis to discover the groupings. Some cladistic work using molecular and morphological character systems is underway in this regard by P. J. Gullan and Lyn Cook (Division of Botany and Zoology, Australian National University, Canberra). Their preliminary findings have been quite interesting and suggest the strong possibility that there will be several genera within what is here treated as *Eriococcus* (Gullan,

personal communication June 17, 1998). Unfortunately, this important research has been underway for only a short period of time and currently includes a small sample of the world eriococcid fauna.

For many years, the first author surmised that the unusually large tubular ducts present on *E. buxi* (Fonscolombe) and *E. eucalypti* Maskell were sufficient to characterize *Eriococcus* as separate from *Acanthococcus* (see Miller and Williams 1976). However, it now appears that this is not necessarily the case and for the purposes of this paper we accept the conservative view pending results of the research by Gullan and her colleagues. This conservative view is consistent with the research of Ferris (1957), Hoy (1963), and Williams (1985) and places all or most of the questionable genera in the genus *Eriococcus*. With this in mind, it is necessary to move several species previously placed in *Acanthococcus* into the genus *Eriococcus* for the first time.

New Combinations in the Eriococcidae

Eriococcus abaii (Danzig), **n. comb.**
Acanthococcus abaii Danzig 1990: 373.

Eriococcus actius (Miller & Miller), **n. comb.**
Acanthococcus actius Miller & Miller 1993: 9.

Eriococcus adzharicus (Hadzibejli), **n. comb.**
Acanthococcus adzharicus Hadzibejli 1960: 310.

Eriococcus arenariae (Miller & Miller), **n. comb.**
Acanthococcus arenariae Miller & Miller 1993: 13.

Eriococcus barri (Miller), **n. comb.**
Acanthococcus barri Miller 1991: 337.

Eriococcus beshearae (Miller & Miller), **n. comb.**
Acanthococcus beshearae Miller & Miller 1993: 15.

Eriococcus brachypodii (Borchsenius & Danzig), **n. comb**.
Greenisca brachypodii Borchsenius & Danzig 1966: 43.

Eriococcus centaureae (Savescu), **n. comb.**
Acanthococcus centaureae Savescu 1985: 122.

Eriococcus danzigae (Miller & Gimpel), **n. comb**.
Rhizococcus confusus Danzig 1962a: 854 (junior secondary homonym).
Acanthococcus danzigae Miller & Gimpel 1996: 600 (replacement name).

Remarks: The replacement name *A. danzigae* was given for *Rhizococcus confusus* Danzig (1962a) when it was transferred to *Acanthococcus* by Miller & Gimpel (1996) making it a junior secondary homonym of *A. confusus* (Maskell) (1892). The species epithet *danzigae* must continue to be used when transferred to *Eriococcus*, since *A. confusus* (Maskell) also is placed in *Eriococcus* and is the senior homonym.

Eriococcus davidsoni (Miller & Miller), **n. comb.**
Acanthococcus davidsoni Miller & Miller 1993: 25.

Eriococcus dennoi (Miller & Miller), **n. comb.**
Acanthococcus dennoi Miller & Miller 1993: 27.

Eriococcus droserae (Miller, Liu, and Howell), **n. comb.**
Acanthococcus droserae Miller, Liu, and Howell 1992: 512.

Eriococcus epacrotrichus (Miller & Miller), **n. comb.**
Acanthococcus epacrotrichus Miller & Miller 1992: 33.

Eriococcus evelinae (Kozár), **n. comb.**
Rhizococcus evelinae Kozár 1983: 144.
Acanthococcus evelinae (Kozár); Miller & Gimpel 1996: 600.

Eriococcus froebeae (Miller), **n. comb.**
Acanthococcus froebeae Miller 1991: 343.

Eriococcus herbaceus (Danzig), **n. comb.**

Rhizococcus herbaceus Danzig 1962b: 22.

Acanthococcus herbaceus; Nast et al. 1990: 120.

Acanthococcus herbaceus; Tereznikova 1981: 29.

Eriococcus hoyi (Miller & Miller), **n. comb.**

Acanthococcus hoyi Miller & Miller 1992: 44.

Eriococcus iljiniae (Danzig), **n. comb.**

Rhizococcus iljiniae Danzig 1972: 339.

Acanthococcus iljiniae; Miller & Gimpel 1996: 601.

Eriococcus istriensis (Kozár), **n. comb.**

Gregoporia istriensis Kozár 1983: 142.

Acanthococcus istriensis; Miller & Gimpel 1996: 601.

Eriococcus korotyaevi (Danzig), **n. comb.**

Acanthococcus korotyaevi Danzig 1982: 145.

Eriococcus laeticoris (Tereznikova), **n. comb.**

Greenisca laeticoris Tereznikova 1965: 975.

Kaweckia laeticoris; Koteja & Zak-Ogaza 1981: 507.

Neokaweckia laeticoris; Tang & Hao 1995: 514.

Acanthococcus laeticoris; Miller & Gimpel 1996: 601.

Eriococcus leptoporus (Miller & Miller), **n. comb.**

Acanthococcus leptoporus Miller & Miller 1993: 39.

Eriococcus mackenziei (Miller & Miller), **n. comb.**

Acanthococcus mackenziei Miller & Miller 1992: 60.

Eriococcus macrobactrus (Miller & Miller), **n. comb.**

Acanthococcus macrobactrus Miller & Miller 1992: 62.

Eriococcus matesovae (Miller & Gimpel), **n. comb.**

Acanthococcus multispinosus Matesova 1976: 24 (junior secondary homonym).

Acanthococcus matesovae Miller & Gimpel 1996: 600 (replacement name).

Remarks: The replacement name *A. matesovae* was given for *Acanthococcus multispinosus* Matesova (1976) when it was transferred to *Acanthococcus* by Miller & Gimpel (1996) making it a junior secondary homonym of *A. multispinosus* Kuhlgatz (1898). The species epithet *matesovae* must continue to be used when transferred to *Eriococcus*, since *A. multispinosus* Kulgatz also is placed in *Eriococcus* and is the senior homonym.

Eriococcus megaporus (Miller & Miller), **n. comb.**

Acanthococcus megaporus Miller & Miller 1993: 45.

Eriococcus mesotrichus (Miller & Miller), **n. comb.**

Acanthococcus mesotrichus Miller & Miller 1993: 48.

Eriococcus microtrichus (Miller & Miller), **n. comb.**

Acanthococcus microtrichus Miller & Miller 1992: 65.

Eriococcus minimus (Tang & Li), **n. comb.**

Acanthococcus minimus Tang & Li 1988: 71.

Rhizococcus minimus; Tang & Hao 1995: 352.

Eriococcus monotrichus (Miller & Miller), **n. comb.**

Acanthococcus microtrichus Miller & Miller 1993: 54.

Eriococcus multispinatus (Tang & Hao), **n. comb.**

Rhizococcus multispinatus Tang & Hao 1995: 598.

Acanthococcus multispinatus; Miller & Gimpel 1996: 602.

Eriococcus oligacanthus (Danzig), **n. comb.**

Rhizococcus oligacanthus Danzig 1972: 341.

Acanthococcus oligacanthus; Miller & Gimpel 1996: 602.

Eriococcus oligotrichus (Miller & Miller), **n. comb.**
Acanthococcus oligotrichus Miller & Miller 1993: 57.
Eriococcus ophius (Miller & Miller), **n. comb.**
Acanthococcus ophius Miller & Miller 1993: 59.
Eriococcus orientalis (Borchsenius), **n. comb.**
Greenisca orientalis Borchsenius 1956: 676.
Kaweckia orientalis (Borchsenius); Tang & Hao 1995: 511.
Acanthococcus orientalis (Borchsenius); Miller & Gimpel 1996: 602.
Eriococcus oxyacanthus (Danzig), **n. comb.**
Acanthococcus oxyacanthus Danzig 1975: 55.
Rhizococcus oxyacanthus; Kozár & Walter 1985: 75.
Eriococcus rubrus (Matesova), **n. comb.**
Greenisca rubra Matesova 1960: 209.
Kaweckia rubra; Koteja & Zak-Ogaza 1981: 508.
Neokaweckia rubra; Tang & Hao 1995: 515.
Acanthococcus rubra; Miller & Gimpel 1996: 603.
Eriococcus salicicola Tang, **nomen nudum**

Remarks: Tang (1984) indicated that this species occurs widely over northeastern China on willow. He stated that he would be describing the species as new in the future, but there is no record of its publication.

Eriococcus stauroporus (Miller & Miller), **n. comb.**
Acanthococcus stauroporus Miller & Miller 1992: 82.
Eriococcus tosotrichus (Miller & Miller), **n. comb.**
Acanthococcus tosotrichus Miller & Miller 1993: 62.
Eriococcus washingtonensis (Miller & Miller), **n. comb.**
Acanthococcus washingtonensis Miller & Miller 1992: 90.
Eriococcus whiteheadi (Miller), **n. comb.**
Acanthococcus whiteheadi Miller 1991: 350.
Eriococcus zernae (Tereznikova), **n. comb.**
Acanthococcus zernae Tereznikova 1977: 571.

New Generic Synonymy in the Eriococcidae

Neokaweckia Tang & Hao 1995: 596, **new synonymy**

Type species: *Greenisca rubra* Matesova 1960, by monotypy and original designation

Remarks: This genus is characterized by having a small anal ring, truncate body setae that are restricted to the last abdominal segments, and dorsal cruciform pores. These characters are considered to be within the expected range of variation for the genus *Eriococcus*.

New Generic Homonomy and Replacement Name in the Eriococcidae

***Neotrichococcus* Miller & Gimpel, new replacement name**
Trichococcus Borchsenius 1948: 503.

Type species: *Trichococcus filifer* Borchsenius 1948, by monotypy and original designation.

Remarks: *Trichococcus* Borchsenius is a junior homonym of *Trichococcus* Kanda (1941) which is now considered to be a junior synonym of *Beesonia* Green. Morrison and Morrison (1966) first discovered this homonymy but did not provide a replacement name.

Neotrichococcus filifer (Borchsenius), **n. comb.**
Trichococcus filifer Borchsenius 1948: 503.

Family Transfer of Cancerococcus to the Margarodidae

Cancerococcus Koteja 1988: 412, **new family assignment**

Remarks: This monotypic genus was originally placed in the Eriococcidae presumably because of the enlarged setae on the antennae, a character found in many eriococcid males. However, we have discovered that the genus is most closely related to the Pityococcini genera *Pityococcus* (McKenzie 1942) (including the species *P. ferrisi* McKenzie, *P. deleoni* McKenzie, *P. rugulosus* McKenzie) and *Desmococcus* (*D. captivus* McKenzie and *D. sedentarius* McKenzie) and is here transferred to the Margardodidae. The description of *Cancerococcus* (Koteja 1988) is based on a single wingless male from amber. The illustrations and description provided by Koteja were compared with a single undetermined male of *Pityococcus* deposited in the collection of National Museum of Natural History, Beltsville, Maryland. The following similarities occur in both taxa: Numerous short setae on the antennae; penial sheath that is apically bifurcate and has a broad aedeagus; antennae with short, round segments; eyes apparently numbering 4 (*C. apterous*) or 5 (*Pityococcus* sp.) on each side of the head and set on a plate. This combination of characters is unique to the Pityococcini in the Margarodidae.

New Synonymy in the Cerococcidae

Asterococcus ramakrishnai (Ramakrishna Ayyar)

Cerococcus ramakrishnae Ramachanran & Ramakrishna Ayyar 1934: 86. (nomen nudum)

Cerococcus ramakrishnae Ramakrishna Ayyar 1936: 148.

Asterococcus ramakrishnai Lambdin 1983: 304–306, **new homonymy and synonymy**.

Remarks: The original combination of *Cerococcus ramakrishnae* is an unpublished manuscript name of Green. Ramachanran & Ramakrishna Ayyar (1934) cited the name but gave no description thus creating a nomen nudum. Ramakrishna Ayyar (1936) did not realize that he was validating the name and describing it after himself, but this was the case. Lambdin (1983) apparently knew of Green's manuscript name, but did not realize that Ramakrishna's description was valid and described the species as new. Lambdin also corrected the spelling of the species epithet from "*ramakrishnae*" to "*ramakrishnai*" and moved the species from *Cerococcus* to *Asterococcus*. From the syntypes of *Cerococcus ramakrishnae*, we have chosen and marked as lectotype an adult female labeled in Green's handwriting: "on Ficus rootlets/ India, (Coimbatore)/ coll. Ramakrishna/ 24/ 31. No. 335." (BMNH). The slide contains three specimens; the center specimen is the lectotype. There are three paralectotypes.

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101(1), 1999, pp. 219–220

NOTE

Scaphytopius angustatus (Osborn) (Homoptera: Cicadellidae), a Leafhopper Characteristic of Pitch Pine-Scrub Oak Barrens

Scaphytopius angustatus (Osborn), a widely distributed Nearctic leafhopper of the deltocephaline tribe Scaphytopiini, is the only known conifer-feeding member of the genus (Hepner. 1947. University of Kansas Science Bulletin 31: 413–541). Adults are about 4 to 5 mm long, pale greenish fulvous or greenish yellow, with subhyaline forewings; the distinctive male genitalia should be examined for positive identification (Hepner 1947; Berine. 1952. Canadian Entomologist 84: 311–313; 1956. Canadian Entomologist 88(Supplement 2): 1–180). This pine specialist has been recorded from jack pine (*Pinus banksiana* Lamb.), red pine (*P. resinosa* Aiton), and pitch pine (*P. rigida* Mill.) (Ball. 1932. Canadian Entomologist 64: 251–255; Hepner 1947). Ecological information otherwise is lacking for this infrequently collected species.

During studies of mirids (Wheeler. 1991. Journal of the New York Entomological Society 99: 405–440) and fulgoroids (Wheeler and Wilson. 1996. Proceedings of the Entomological Society of Washington 98: 100–108) inhabiting pitch pine-scrub oak barrens, I found *S. angustatus* to be a characteristic insect of northeastern pine barrens—that is, occurring consistently in, but not restricted to, that community type. It is one of several leafhopper species found on pitch pine in pine barrens. Individuals of the leafhopper were beaten from branches of pines, mainly pitch pine, as described by Wheeler (1991) for mirids occurring on scrub oak (*Quercus ilicifolia* Wangenh.). Voucher specimens have been deposited in the collections of Cornell University, Ithaca, N.Y.; National Museum of Natural History, Washington, D.C.; and the Pennsylvania Department of Agriculture, Harrisburg.

Once considered a "distinctly northern species" (DeLong. 1923. pp. 56–163 *In* Britton, W.E., ed., The Hemiptera or Sucking Insects of Connecticut. Connecticut Geological and Natural History Survey Bulletin 34), *S. angustatus* is now known as far south as Georgia. Other records include Maine, Massachusetts, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Ontario, Pennsylvania, South Carolina, Virginia, and Wisconsin (Metcalf. 1967. pp. 2,075–2,695 *In* General Catalogue of the Homoptera, Fascicle VI, Part 10, USDA ARS, Washington, D.C.). Metcalf (1967) also listed Connecticut, but in a treatment of that state's leafhopper fauna, *S. angustatus* was only predicted to be found there (DeLong 1923).

During 1991–1995, I collected *S. angustatus* at 21 sites, ranging from extensive pitch pine-scrub oak barrens, such as Waterboro in Maine, Ossipee in New Hampshire, New York's Shawangunk Mountains, and the New Jersey Pine Barrens, to degraded, remnant pine barrens. Seven collections involved scattered pitch pines in communities other than pine barrens. Collections were made from pitch pine except in the Gadway Barrens, Clinton Co., N.Y., where jack pine was the host. New state records are Connecticut, Rhode Island, and Vermont. Numbers in parentheses refer to adults unless otherwise stated.

CONNECTICUT: Hartford Co., Shaker Pines, Enfield, 28 Sept. 1991 (3). MAINE: York Co., Biddeford, 14 Aug. 1993 (2); Kennebunk Plains, 13 Aug. 1993 (1); Waterboro Barrens Preserve, 8 Aug. 1995 (1, 15 nymphs). MASSACHUSETTS: Franklin Co., Montague sand plains, 14 Sept. 1991 (1), 15 Aug. 1993 (3, 1 nymph). NEW

HAMPSHIRE: Carroll Co., Ossipee Pine Barrens, 7 Aug. 1995 (6 nymphs); Hillsborough Co., Amherst (1) & Nashua (1), 6 Aug. 1995; Brookline, 14 Sept. 1991 (1). NEW JERSEY: Burlington Co., NW. of Warren Grove, 11 Aug. 1991 (2). NEW YORK: Albany Co., remnant barrens near Pine Bush Preserve, 22 Aug. 1993 (1); Clinton Co., NE. of Ausable Chasm, 30 Aug. 1992 (1); Gadway Barrens, S. of Cannon Corners, 21 Aug. 1993 (1); West Chazy Barrens, 29 Aug. 1992 (2); Jefferson Co., Plessis, 16 Aug. 1992 (>20 adults and nymphs); Saratoga Co., 3 mi. S. of South Glens Falls, 22 Aug. 1992 (1); Ulster Co., Mohonk Perserve near New Paltz, 29 Sept. 1991 (2), 21 Aug. 1992 (3), 20 Aug. 1993 (1). PENNSYLVANIA: Luzerne Co., Humboldt Industrial Park SW. of Hazleton, 22 Aug. 1993 (1); Schuylkill Co., near Frackville, 6 Oct. 1991 (1). RHODE ISLAND: Providence Co., Slatersville, 19 Sept. 1992 (2); Washington Co., near Arcadia Management Area, 1 Sept. 1991 (2). VERMONT: Chittenden Co., Camp Johnson, Colchester, 28 Aug. 1992 (1).

Nymphs were seldom observed, and only the mostly bright green fifth instars were detected, earlier instars perhaps having been overlooked in the beating net. Because nymphs were not observed before August and no adults were taken during extensive spring and early-summer sampling of pitch pine, *S. angustatus* likely overwinters in the egg stage.

Adults of this late-season, apparently univoltine leafhopper were observed in pine barrens from early August until early October. In the northern part of its range (OH, NH, NY, WI), *S. angustatus* has been reported only from early August (Sanders and DeLong. 1917. Annals of the Entomological Society of America 10: 79–95) to mid-October (Osborn and Knull. 1947. Ohio Journal of Science 46: 329–336), even in New Hampshire, where Lowry (1933. Ohio Journal of Science 33: 59–80) collected leafhoppers nearly throughout the season, beginning in May. In the southern part of the range, adults have been collected in Georgia from June to August (Fattig. 1955. Emory University Museum Bulletin 11: 1–68).

In northeastern pine barrens, I observed *S. angustatus* mainly on seedling and sapling pitch pines and the regrowth from stumps of cut-over trees. Certain other conifer-feeding leafhoppers are associated with seedlings, including those of pitch pine (DeLong, 1926. Ohio Journal of Science 26: 69–72). About a third of the collections of *S. angustatus* were from mature pitch pines, where they often were beaten from bushy growth on the basal whorl of branches, some of which touched the ground. This growth habit, which might be a response to light reflected from the sand, typifies pitch pine in pine barrens (Kelley. 1927. Botanical Gazette 83: 89–93).

I gratefully acknowledge those who accompanied me in the field or enabled me to find pine barrens: Kenneth Adams, Robert Dirig, Paul Huth, Patrick McCarthy, Alan Nye, Dale Schweitzer, Nancy Sferra, and David VanLuven. Christopher Dietrich kindly identified *S. angustatus*, The Nature Conservancy and State Heritage Programs allowed access to several pine barrens, and Peter Adler provided useful comments on an early draft of the manuscript.

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Book Review

Os Mosquitos de Macau (Diptera: Culicidae). Helena Cunha Ramos, Henrique Ribeiro, Maria Teresa Novo, and Emmett R. Easton. 1997. Sociedade Portuguesa de Entomologia, Apartado 8221, P-1800 Lisbon. 201 pp., paper. ISBN 972-97241-0-5.

Among the perquisites of my present position is total access to the world literature on medical entomology. However, despite my databases, I am still occasionally surprised, as by the recent receipt of this lavish monograph on the mosquitoes of Macau (English *Macao,* Mandarin *Aomen*), Portugal's ancient entrepôt on the South China Sea. At the eleventh hour, with Chinese officials poised to take Government House, four widely experienced field biologists from the Centro de Zoologia, Instituto de Investigação Científica Tropical (Cunha Ramos), the Disciplina de Entomologia Médica, Instituto de Higiene e Medicina Tropical, Universidade Nova de Lisboa (Ribeiro and Teresa Novo), and the Centro de Estudos Pré-Universitários, Universidade de Macau (Easton, an expatriate American profiled in *J. New York Entomol. Soc.* 102: 389–391) have joined to forge a faunal survey of continental proportions.

Throughout 1994 and 1995, Cunha Ramos and colleagues scoured peninsular Macau and its offshore islands of Taipa and Coloane, to which the *cidade* is linked by bridges and causeways. In an utterly anthropocentric environment, they secured some 3,000 mosquito specimens representing 28 species (generic and subgeneric abbreviations follow Reinert, *Mosq. Syst.* 7: 105–110, 14: 124–126, 23: 209–210):

Aedes (Finlaya) togoi (Theobald 1907)
Ae. (Stegomyia) albopictus (Skuse 1894)
Ae. (Stg.) w-albus (Theobald 1905)
Anopheles (Anopheles) sinensis Wiedemann 1828
Armigeres (Armigeres) subalbatus (Coquillett 1898)
Ar. (Leicesteria) magnus (Theobald 1908)
Culex (Culex) bitaeniorhynchus Giles 1901
Cx. (Cux.) jacksoni Edwards 1934
Cx. (Cux.) pseudovishnui Colless 1957
Cx. (Cux.) quinquefasciatus Say 1823
Cx. (Cux.) sitiens Wiedemann 1828
Cx. (Cux.) tritaeniorhynchus Giles 1901
Cx. (Cux.) vagans Wiedemann 1828
Cx. (Cux.) vishnui Theobald 1901
Cx. (Culiciomyia) pallidothorax Theobald 1905
Cx. (Eumelanomyia) foliatus Brug 1932
Cx. (Eum.) malayi (Leicester 1908)
Cx. (Lophoceraomyia) infantulus Edwards 1922
Cx. (Lop.) rubithoracis (Leicester 1908)
Cx. (Lop.) sumatranus Brug 1931
Cx. (Lutzia) fuscanus Wiedemann 1820
Cx. (Lut.) halifaxii Theobald 1903
Mansonia (Mansonioides) uniformis (Theobald 1901)
Mimomyia (Mimomyia) chamberlaini Ludlow 1904
Toxorhynchites (Toxorhynchites) macaensis Ribeiro 1997
Tripteroides (Rachionotomyia) aranoides (Theobald 1901)
Uranotaenia (Uranotaenia) annandalei Barraud 1926
Ur. (Ura.) macfarlanei Edwards 1914

Perusal of the regional literature (their bibliography, pp. 195–201, contains 208 entries) yielded seven additional species: *Ae. (Stg.) aegypti* (Linnaeus 1762), *An. (Cellia) jeyporiensis* James 1902, *An. (Cel.) karwari* (James 1902), *An. (Cel.) maculatus* Theobald 1901, *An. (Cel.) minimus* Theobald 1901, *An. (Cel.) tessellatus* Theobald 1901, and *Cx. (Cux.) fuscocephala* Theobald 1907, all thought to occur in Macau in "very low densities." For a territorial total of 35 species, including the just-described

T. macaensis (*J. Am. Mosq. Control Assoc.* 13: 213–217), keys are provided to males, females, and 4th instar larvae. The keys are exceptionally well supported with pen-and-ink drawings, paintings, and stunning color photomicrographs (of 179 numbered illustrations, all but 46 are in full color).

The core of the text (pp. 67–193) is a species-by-species account of mosquito taxonomy, ecology, and distribution. Remarkable in this regard are three full-page, color-coded maps (pp. 68, 84 and 91) that pinpoint collecting sites for each species on Taipa, Coloane, and Macau proper. Thus, it is possible to retrace the authors' steps to particular intersections, ponds, or cramped urban parks, where subsequent generations of the very insects that were the subjects of this study may yet be sought. As guidance to future investigators, photographs of 32 of these sites are included. The vector potential of each species is also assessed for the malarias, 14 arboviruses, human filariases (*Brugia malayi, Wuchereria bancrofti*) and dirofilariases (*Dirofilaria immitis, D. repens*).

A major goal of this endeavor was to compare the diversity of the Macanese mosquito fauna with that of neighboring Hong Kong and the Oriental Region as a whole. To this end, indices of abundance, association and distribution were calculated and are presented as tables throughout the text. These include the distribution of mosquito species in Macau by principal jurisdiction (Table 1); relative breeding indices for each species (Table 2); percentages for utilization of "natural" versus manmade habitats (Table 3); indices of larval association and their statistical significance (Tables 4 and 5); the extraterritorial distribution of each species by zoogeographic region (Table 8); and comparative indices of biodiversity for the mosquito faunas of Macau, Hong Kong, Cameroon, and mainland Portugal (Table 9). Such distillations bespeak countless hours of fieldwork—and countless more of analysis.

The Portuguese are passing now. On 20 December 1999, they will retrocede to China the oldest Western enclave in the Orient. How auspicious, for these two peoples have no quarrel with one another. The Lusitanians will be remembered not for foisting narcotics on a population held hostage, not for having to be forcibly evicted à la Dien Bien Phu, and certainly not for pushing the latest ludicrous cult from the so-called American heartland. Rather, both sides will be left to reflect on over 400 years of mutualism, as evidenced by this oblation.

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101(1), 1999, pp. 222–224

Book Review

The Everglades Handbook: Understanding the Ecosystem. Thomas E. Lodge, introduction by Marjory Stoneman Douglas. 1994, second printing, 1998. St. Lucie Press. xix+228 pp., paper. ISBN 1-884015-06-9. $39.95.

The one person most closely associated with the formation of Everglades National Park was Marjory Stoneman Douglas. Her death earlier this year at 108 years of age marked the end of an important chapter in the history of south Florida. This book provides an introduction to the Everglades, covering all aspects of the region. Mrs. Douglas' short introduction to the book

serves as a brief memorial to her efforts to establish the Park. *The Everglades Handbook: Understanding the Ecosystem* is written from an environmental protectionist perspective, which is to be expected of any work to which Mrs. Douglas contributed.

The book is divided into four parts, each part being divided further into a number of chapters. The first part, *Background*, contains two chapters. Chapter 1, *The Everglades in Space and Time*, describes the geologic history of the Everglades. Chapter 2, *An Ecosystem Review*, is an important chapter for the reader, for it is here that the author defines many terms referring to water and hydrology, including what the Everglades are and are not, and more interestingly, where they are and where they are not. There is a great difference between what the Everglades historically were and what we now think of them as being.

The second part of the book, *Environments of the Everglades Region*, consists of seven chapters, each detailing one aspect of the Everglades. These chapters are weighted toward discussion of plant communities. Chapter 3 describes freshwater marshes, including the plants, soil, water, and effects of weather and fire on the marshes. Chapter 4 discusses tree islands and their importance to the region. Chapter 5 treats hardwood hammocks and Chapter 6 pinelands. Both chapters discuss the role of fire in maintenance of the environment. Chapter 7 is a very interesting discussion of mangrove swamps and their importance to wildlife and fisheries. Chapter 8 describes the vegetation of the coastal lowlands and the effects of hurricanes on south Florida. Finally, Chapter 9 deals with the estuaries and marine waters of the coast. This chapter discusses the flora and geology of Florida Bay and the Gulf of Mexico, and the relationship between oysters and mangroves.

Biogeography of Southern Florida, the third part of the book, probably will be of most interest to entomologists. There are eight chapters in this part of the book, seven of them covering a specific group of animals. Chapter 10 includes such topics as the origin of the biota of southern Florida, and whether south Florida is tropical or subtropical. The Everglades region contains both temperate and tropical plant species, and the origins of each component of the flora are reviewed. Chapter 11 treats the invertebrates, marine, freshwater, and terrestrial. My bias as an entomologist led me to wonder why so few insect species were mentioned, but in fairness there is only one chapter to deal with all invertebrate animals. Among the organisms mentioned are butterflies, crayfish, lobster, shrimp, snails, and spiders. Chapters 12 and 13 cover the fishes. Chapter 12 deals with freshwater species and Chapter 13 with estuarine and marine species. In Chapter 12 the distinction among primary, secondary, and peripheral freshwater fishes is explained. The importance of these fishes to the food chain is mentioned. Chapter 13 summarizes the diversity of the marine and estuarine fishes, and their importance both as game fishes and as a food source for birds. Chapter 14 is a very brief (three and one-half pages) mention of the amphibians of the Everglades. One interesting facet of this chapter is the impact that introduced frogs and toads have had on the native fauna. Chapter 15 considers the reptiles. Most of the chapter deals with crocodilians, although lizards, snakes, tortoises, and turtles are mentioned. Chapter 16 is another very brief chapter that deals with mammals. Almost one entire page is devoted to the Florida panther. Other species receive little attention. The last chapter in this part of the book, Chapter 17, discusses the birds. This chapter devotes much of its space to the large wading birds, which the author admits "attract much attention," and so they do here as well. This is one of the longer chapters in the book, comprising 18 pages. There is only brief mention of passerine birds, raptors, and other types of birds.

The fourth part of the book, *Environmental Impacts*, contains only one chapter, Chapter 18, that describes the effects that

south Florida's increasing population has had on the Everglades. Specimen collecting, off-road vehicles, and introduced species are all mentioned as having adverse impacts on the Everglades. A great portion of the chapter is devoted to the effect that water control projects have had on the Everglades. There is an interesting attempt to bring the global warming controversy into the discussion. However, the author does point out that there is another opinion within the scientific community, that of global cooling. The book ends with speculation on the demise of the Everglades.

The book is extensively footnoted, and contains almost 300 references. The index is superb, permitting the reader to locate passages pertinent to any animal or plant by common or scientific name. The illustrations are of good quality. One disappointment is that all photos are in black-and-white. The author writes in his preface that it was his intention to include a large number of color photographs, but this became impossible due to realities of the publishing business. Many of the photos in the book were taken by photographer Robert Hamer, and their quality and composition leaves one hoping that the color version will some day see print. The shorter chapters are a bit frustrating to read, because the reader is given only enough information to whet the appetite. The shortness of some of the chapters apparently is due to their having been intended originally to accompany the color photos that never were used. The book was not conceived as a textbook, and it is evident that the author did not intend it to be used as one. Readers who want a mathematical treatise detailing the population dynamics of all species in the Everglades will not find that here. For those individuals who have an organismal interest in the Everglades, e.g., naturalists and professional biologists in south Florida, the book will serve as a convenient introduction to some of the more spectacular animals and plants found in the region. For others, the book makes for pleasant reading, but its coverage of the invertebrate fauna is too limited to be of much use to the professional entomologist.

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1999 Meetings of the Entomological Society of Washington

The following programs are scheduled for February to May, 1999. Meetings are at 7:30 PM, the first Thursday of each month, in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

February 4, 1999—Alan Schroeder (U.S. AID), "U.S. AID's Pest Management Activities in Africa."

March 4, 1999—Dale F. Schweitzer (The Nature Conservancy, Port Norris, NJ), "Lepidoptera and Other Insects in the New Jersey Pine Barrens."

April 1, 1999—Ted R. Schultz (Smithsonian Institution), "The Natural History of Fungus-Growing Ants."

May 6, 1999—Joseph V. McHugh (University of Georgia), "A Phylogenetic Analysis of Erotylidae (Coleoptera) with Implications for the Evolution of Their Mycophagy."

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DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA IMPERFECTA* (COQUILLETT) (DIPTERA: TEPHRITIDAE)

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Abstract.—The egg, first-, second- and third-instar larvae, and puparium of *Trupanea imperfecta* (Coquillett), a monophagous, bi- or trivoltine tephritid principally reproducing in flower heads of *Bebbia juncea* (Bentham) Greene (Asteraceae) in southern California, are described and figured for the first time. The egg pedicel is composed mainly of a single row of large aeropyles. As with the other *Trupanea* species previously studied, the lateral spiracular complex of the third instar is unique to *T. imperfecta,* with a stelex sensillum and two verruciform sensilla on the metathorax, and two verruciform sensilla on the abdominal segments. The third instar of *T. imperfecta* very closely resembles *T. arizonensis* Malloch in general habitus and sensory structures.

Key Words: Insecta, *Trupanea,* Asteraceae, nonfrugivorous Tephritidae, taxonomy of immature stages, egg, larva, puparium

The life history of *Trupanea imperfecta* (Coquillett) (Diptera: Tephritidae) was described by Goeden (1988) before adoption of our current format incorporating description of the immature stages. To correct this deficiency and allow full comparison with the 36 species of southern California nonfrugivorous fruit flies for which life histories and descriptions of the immature stages have now been published, this paper describes the immature stages of *T. imperfecta.*

MATERIALS AND METHODS

One-liter samples of excised, immature and mature flower heads from the main host of *T. imperfecta, Bebbia juncea* (Bentham) Greene (Asteraceae), potentially containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-two eggs, 23 first-, 14 second-, and nine third-instar larvae, and nine puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG SEM in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Plant names used in this paper follow Munz (1974); tephritid names follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996), Goeden and Teerink (1997, 1998, 1999), Goeden et al. (1998a, b), and Teerink and Goeden (1998), and our earlier works cited therein. Means

± SE are used throughout this paper. Voucher specimens of *T. imperfecta* eggs, larvae and puparia are stored in a collection of immature Tephritidae acquired by JAT and now maintained by RDG.

Results and Discussion

Taxonomy

Immature stages.—The egg and puparium of *T. imperfecta* were described and photographs of these stages and larvae were provided by Goeden (1988), but detailed descriptions based on scanning electron microscopy heretofore have not been published.

Egg: The egg (Fig. 1A) of *T. imperfecta* has a short pedicel circumscribed by a single row of subrectangular aeropyles so large that they uniquely occupy more than half of this structure (Fig. 1B). The micropyle is located on the anterior end of the pedicel (Fig. 1C-1).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 2A); gnathocephalon smooth, lacking rugose pads (Fig. 2C); dorsal sensory organ a dome-shaped papilla (Fig. 2B-1); subdorsal sensillum located laterad of dorsal sensory organ (Fig. 2B-2); anterior sensory lobe bears terminal sensory organ (Fig. 2B-3), lateral sensory organ (Fig. 2B-4) and supralateral sensory organ (Fig. 2B-5); stomal sense organ ventrad of anterior sensory lobe (Fig. 2C-1); mouth hooks bidentate (Fig. 2C-2); median oral lobe laterally flattened (Fig. 2C-3); a pair of integumental petals dorsad of mouth hooks (Fig. 2C-4); pit sensillum laterad of mouth lumen (Fig. 2C-5); minute acanthae ventrad of mouth lumen (Fig. 2C-6); anterior spiracle absent; abdominal lateral spiracular complex consists of a spiracle and two verruciform sensilla; caudal segment with two stelex sensilla dorsad and ventrad of posterior spiracular plates (Fig. 2D-1); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 2D-2); posterior spiracular plate bears two ovoid rimae, ca. 0.008 mm in length (Fig. 2D-3), and four interspiracular processes, each with 1–3 branches, longest measuring 0.010 mm (Fig. 2D-4); intermediate sensory complex consists of a stelex sensillum (Fig. 2D-5) and a medusoid sensillum (Fig. 2D-6).

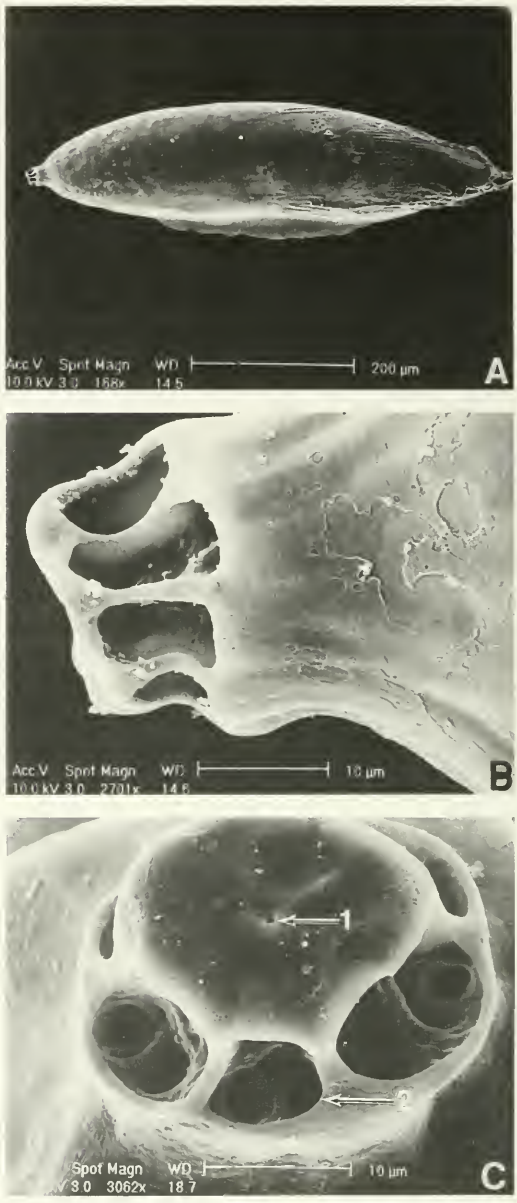

Fig. 1. Egg of *Trupanea imperfecta:* (A) habitus, pedicel to left; (B) egg pedicel; (C) pedicel, anterior view, 1—micropyle, 2—aeropyle.

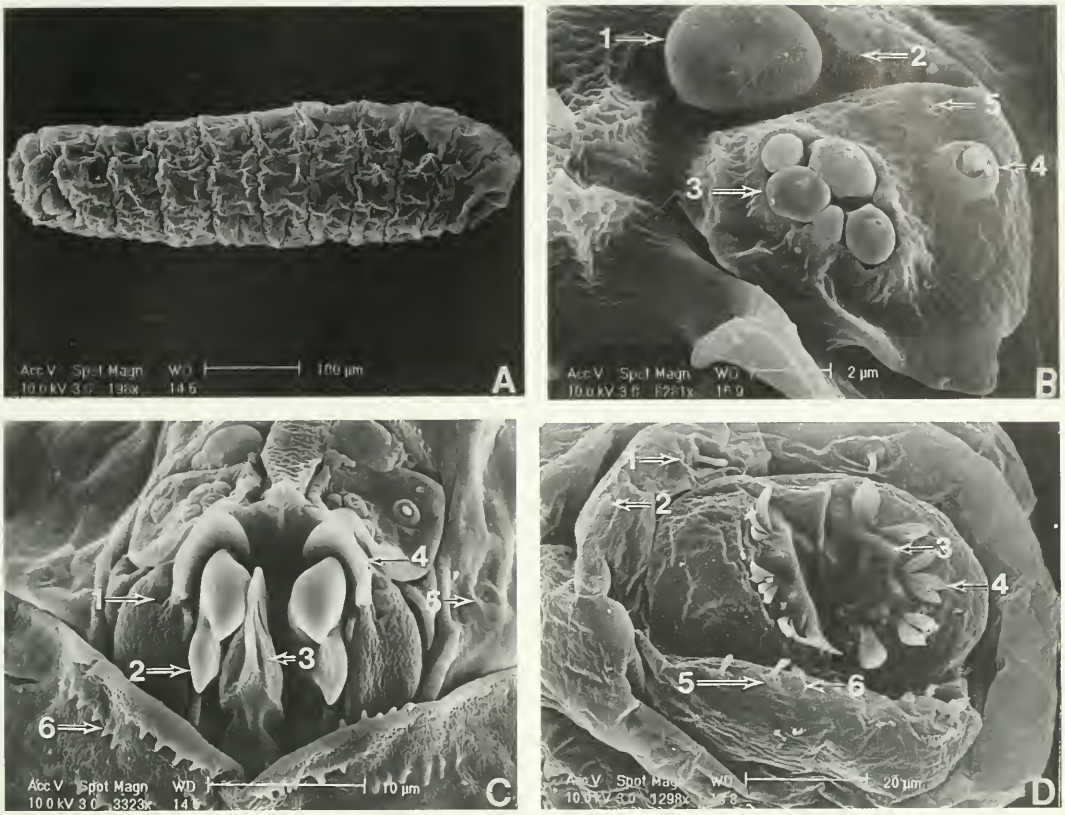

Fig. 2. First instar of *Trupanea imperfecta:* (A) habitus, anterior end to right; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—subdorsal sensillum, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (C) gnathocephalon, anterior view, 1—stomal sense organ, 2—mouth hook, 3—median oral lobe, 4—integumental petal, 5—pit sensillum, 6—minute acanthae; (D) caudal segment, 1—stelex sensillum, 2—verruciform sensillum, 3—rima, 4—interspiracular process, 5—intermediate sensory complex, stelex sensillum, 6—intermediate sensory complex, medusoid sensillum.

Second instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 3A); gnathocephalon conical; rugose pads laterad of anterior sensory lobe (Fig. 3B-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-1); anterior sensory lobe bears terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-3, 3C-6); mouth hooks bidentate (Fig. 3D-1); median oral lobe laterally flattened (Fig. 3D-2); labial lobe attached to median oral lobe (Fig. 3D-3); six pit sensilla circumscribe gnathocephalon (Fig. 3B-4); minute acanthae circumscribe anterior margin of prothorax (Fig. 3E-1); rugose pads (Fig. 3E-2) and two rows of verruciform sensilla circumscribe prothorax (Fig. 3E-3); anterior thoracic spiracles bear 3 rounded papillae (Fig. 3E-4); lateral spiracular complex not seen; caudal segment with minute acanthae dorsally (Fig. 3F-1); two stelex sensilla dorsad and ventrad of posterior spiracular plates (Fig. 3F-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 3F-3); posterior spiracular plate bears three ovoid rimae, ca. 0.021 mm in length (Fig. 3F-4), and four interspiracular processes, each with 1–2 branches, longest measuring 0.013 mm (Fig. 3F-5); intermediate sensory complex

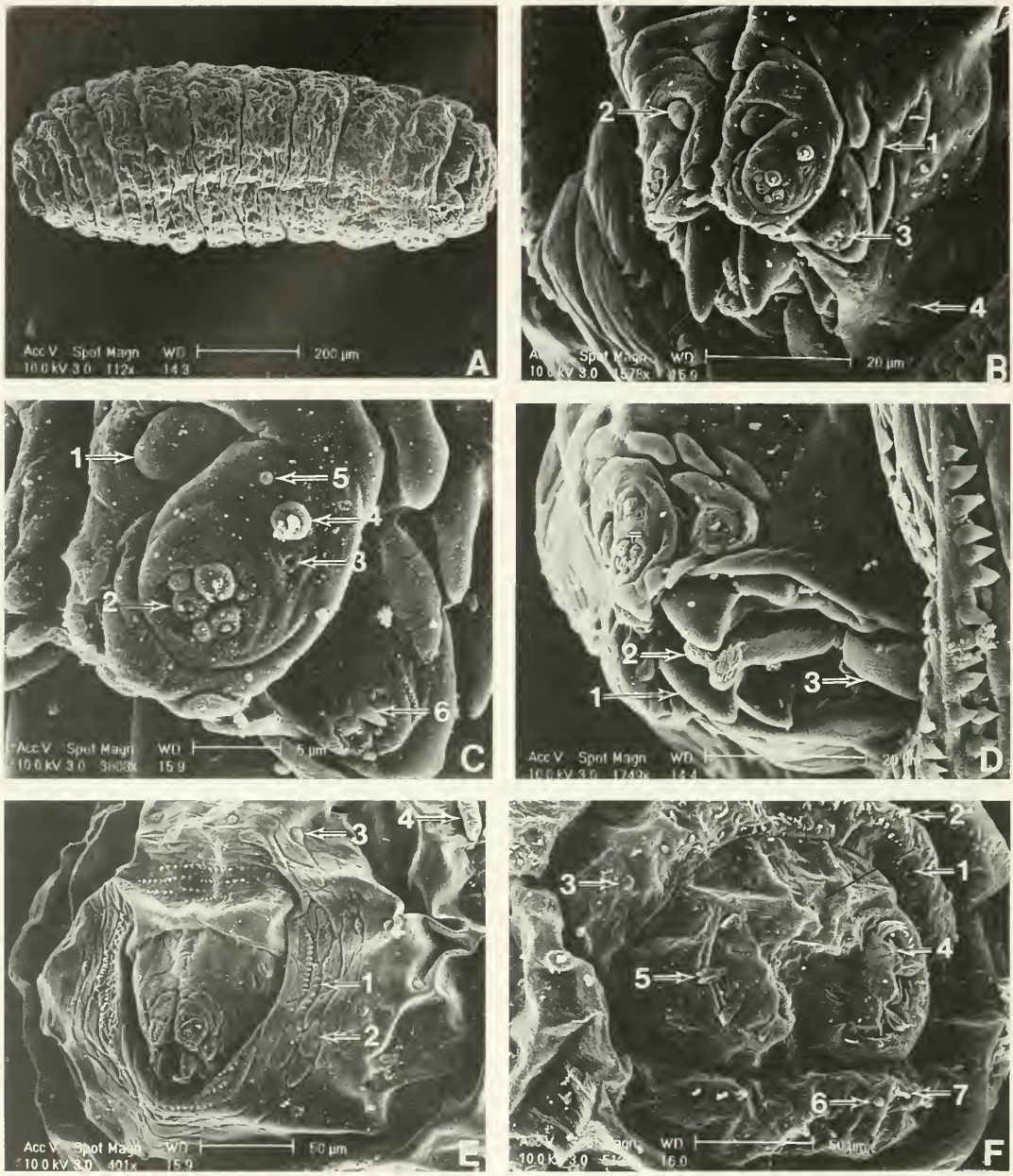

Fig. 3. Second instar of *Trupanea imperfecta:* (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—rugose pad, 2—dorsal sensory organ, 3—stomal sense organ, 4—pit sensillum; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (D) gnathocephalon, ventral view, 1—mouth hooks, 2—median oral lobe, 3—labial lobe; (E) gnathocephalon, prothorax, anterolateral view, 1—minute acanthae, 2—rugose pads, 3—verruciform sensillum, 4—anterior thoracic spiracle; (F) caudal segment, 1—minute acanthae, 2—stelex sensillum, 3—verruciform sensillum, 4—rima, 5—interspiracular process, 6—intermediate sensory complex, medusoid sensillum, 7—intermediate sensory complex, stelex sensillum.

consisting of a medusoid sensillum (Fig. 3F-6) and a stelex sensillum (Fig. 3F-7).

Third instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 4A); gnathocephalon conical (Fig. 4B), rugose pads laterad of anterior sensory lobe (Fig. 4B-1), those laterad of mouth lumen serrated on ventral margin (Fig. 4C-1); dorsal sensory organ a dome-shaped papilla (Fig. 4B-2, 4C-2); subdorsal sensillum laterad of dorsal sensory organ; anterior sensory lobe (Fig. 4B-3, 4C) bears terminal sensory organ (Fig. 4C-3), pit sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), and supralateral sensory organ (Fig. 4C-6); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 4B-4, 4C-7); mouth hooks tridentate (Fig. 4B-5); median oral lobe laterally flattened, tapering anteriorly (Fig. 4B-6); prothorax circumscribed anteriorly with minute acanthae (Fig. 4D-1); rugose pads circumscribe prothorax posteriorad to minute acanthae (Fig. 4D-2); two rows of verruciform sensilla circumscribe prothorax posteriorad to rugose pads (Fig. 4D-3); stelex sensillum located dorsomedially (Fig. 4D-4); anterior thoracic spiracle bears three rounded papillae (Fig. 4D-5); mesothorax and metathorax circumscribed anteriorly with verruciform sensilla; metathoracic lateral spiracular complex consists of a spiracle (Fig. 4E-1), a stelex sensillum (Fig. 4E-2), and two verruciform sensilla (Fig. 4E-3); abdominal lateral spiracular complex consists of a spiracle (Fig. 4F-1) and two verruciform sensilla (Fig. 4F-2); caudal segment circumscribed by minute acanthae; two stelex sensilla dorsad and ventrad of posterior spiracular plates (Fig. 4G-1); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 4G-2); posterior spiracular plate bears three ovoid rimae, ca. 0.03 mm in length (Fig. 4G-3), and four interspiracular processes, each with 2–4 branches, longest measuring 0.02 mm (Fig. 4G-4); intermediate sensory complex consists of a medusoid sensillum (Fig. 4H-1), and a stelex sensillum (Fig. 4H-2).

Puparium: Black, elongate-cylindrical (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1), and anterior spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae (Fig. 5C-1), two stelex sensilla dorsad and ventrad of posterior spiracular plates (Fig. 5C-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 5C-3); posterior spiracular plate bears three ovoid rimae (Fig. 5C-4), and four interspiracular processes, each with 2–4 branches (Fig. 5C-5); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum (Fig. 5C-6).

Discussion

The egg of *Trupanea imperfecta* is elongate-ellipsoidal, with a reduced peg-like anterior pedicel (Goeden 1988). It is similar in size and shape to *T. signata* Foote (Goeden and Teerink 1997), longer than *T. actinobola* (Loew) (Goeden et al. 1998b), *T. californica* Malloch (Headrick and Goeden 1991), and *T. pseudovicina* Hering (Goeden and Teerink 1998), and shorter but wider than *T. arizonensis* (Goeden and Teerink 1999). The pedicel is mainly composed of large aeropyles (Figure 1B, 1C). The pedicels of *T. arizonensis, T. jonesi* Curran, *T. nigricornis* (Coquillett), and *T. pseudovicina* are similar in shape, but have smaller aeropyles spaced farther apart (Goeden and Teerink 1998, 1999; Goeden et al. 1998a; Knio et al. 1996).

The first instar of *T. imperfecta* is similar in general habitus to previously studied *Trupanea* species (Goeden and Teerink 1998, 1999; Goeden et al. 1998a, b; Knio et al. 1996; Teerink and Goeden 1998). The gnathocephalon is smooth, lacking rugose pads. The pit sensory organ is indistinct on the anterior sensory lobe, and the stomal sense organ is also indistinct. Minute acanthae are limited to the ventral margin of the prothorax. The interspiracular processes, each with 1–3 blade-like processes, are similar to *T. actinobola, T. bisetosa* (Coquil-

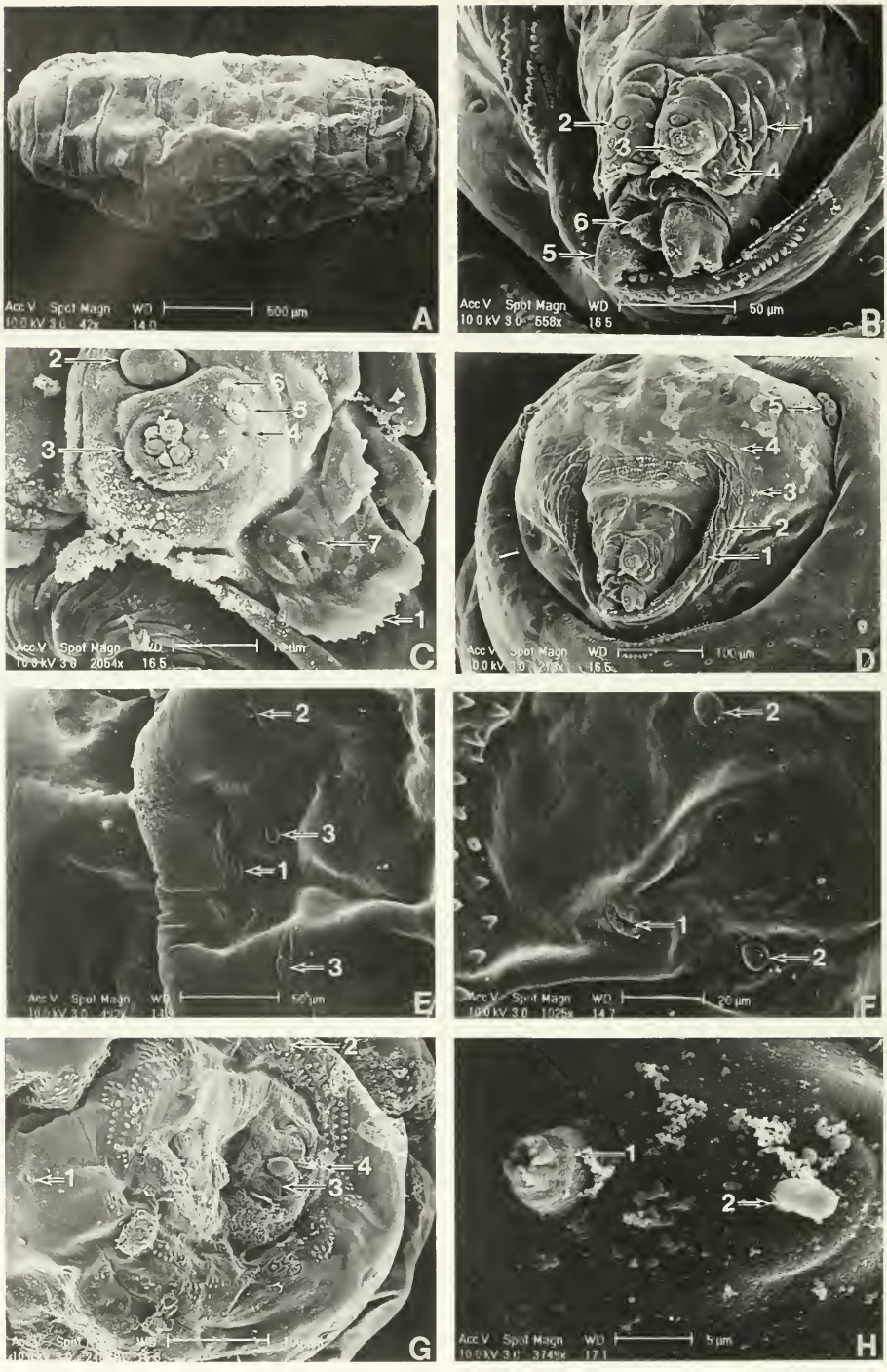

Fig. 4. Third instar of *Trupanea imperfecta:* (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—rugose pads, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—stomal sense organ, 5—mouth hook, 6—median oral lobe; (C) anterior sensory lobe, 1—serrated rugose pad, 2—dorsal sensory organ, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—stomal sense organ; (D) gnathocephalon, prothorax, anterior view, 1—minute acanthae, 2—rugose pad, 3—verruciform sensillum, 4—stelex sensillum, 5—anterior thoracic spiracle; (E) metathorax, 1—spiracle, 2—stelex

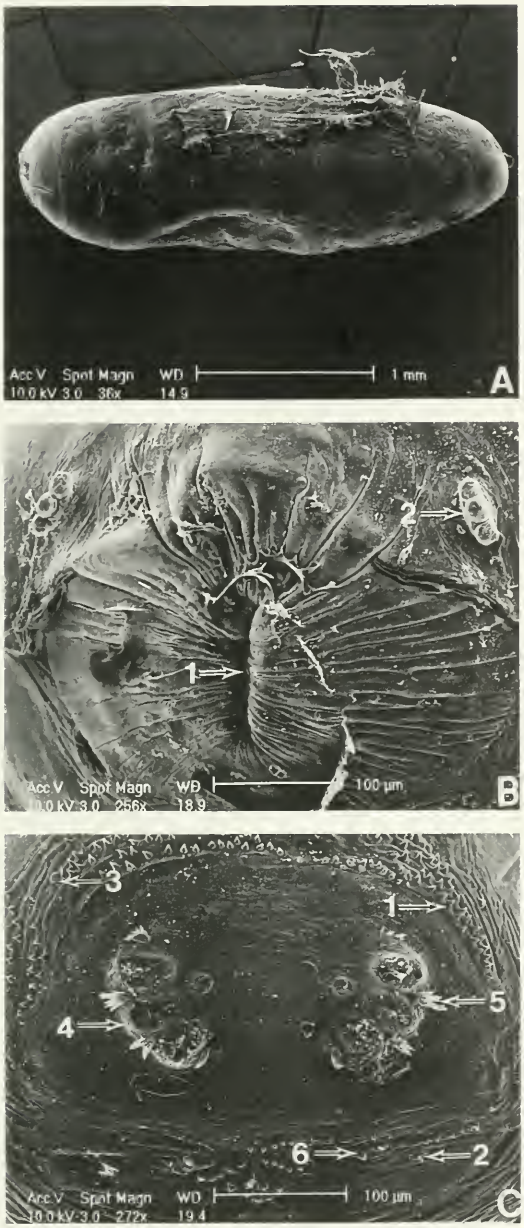

Fig. 5. Puparium of *Trupanea imperfecta:* (A) habitus, anterior end to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—minute acanthae, 2—stelex sensillum, 3—verruciform sensillum, 4—rima, 5—interspiracular process, 6—intermediate sensory complex.

lett), and *T. pseudovicina* (Goeden and Teerink 1998; Goeden et al. 1998b; Knio et al. 1996).

The second instar of *T. imperfecta* differs from the first instar in possessing rugose pads laterad of the mouth lumen, and the anterior margin of the prothorax is circumscribed by minute acanthae, rugose pads, and two rows of verruciform sensilla. All four of the anterior sensory lobe sensilla, as well as the stomal sense organ, are distinct in the second instar. The anterior thoracic spiracle is present in the second instar, and the posterior spiracular plates possess three ovoid rimae rather than two as in the first instar. The caudal segment in the second instar, unlike in the first instar, is circumscribed by minute acanthae.

The third instar differs from the second instar in possessing serrated rugose pads laterad of the mouth lumen, and the mouth hooks tridentate. The third instar of *T. imperfecta* is very similar in general habitus to *T. arizonensis* and *T. pseudovicina,* being more elongate-cylindrical than barrel-shaped (Goeden and Teerink 1998, 1999). *Trupanea imperfecta* and *T. arizonensis* are also similar, in that the meso- and metathorax are circumscribed by verruciform sensilla and the anterior thoracic spiracle bears three ovoid papillae (Goeden and Teerink 1998). However, there are slight differences between these two species in that the rugose pads laterad of the mouth lumen are serrated in *T. imperfecta,* but not in *T. arizonensis.* Moreover, the metathoracic lateral spiracular complex is slightly different, with a stelex sensillum and two verruciform sensilla in *T. imperfecta,* and three verruciform sensilla in *T. arizonensis* (Goeden and Teerink 1999). *Trupanea pseudovicina* is similar to *T. imperfecta* in having serrated rugose pads laterad of the mouth lumen (Goe-

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sensillum, 3—verruciform sensilla; (F) sixth abdominal segment, 1—spiracle, 2—verruciform sensilla: (G) caudal segment, 1—stelex sensillum, 2—verruciform sensillum, 3—rima, 4—interspiracular process; (H) intermediate sensory complex, 1—medusoid sensillum, 2—stelex sensillum.

den and Teerink 1998). It differs from *T. imperfecta* by having four, not three, papillae on the anterior spiracle; the meso- and metathorax not circumscribed by verruciform sensilla, and a stelex sensillum and two, not one, verruciform sensilla in the metathoracic lateral spiracular complex (Goeden and Teerink 1998). As with the other *Trupanea* species studied by us to date, the lateral spiracular complex is unique to *T. imperfecta* (Goeden and Teerink 1997, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996, Teerink and Goeden 1997).

The puparium of *T. imperfecta* is larger than *T. actinobola* and *T. californica* (Goeden et al. 1998b; Headrick and Goeden 1991), wider but shorter than *T. arizonensis* and *T. pseudovicina* (Goeden and Teerink 1998, 1999).

Acknowledgments

We are grateful to David Headrick for his helpful comments on an earlier draft of this paper.

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THE MICROCADDISFLY GENUS *ITHYTRICHIA* EATON (TRICHOPTERA: HYDROPTILIDAE) IN NORTH AMERICA

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Abstract.—The distribution and taxonomy of the microcaddisfly genus *Ithytrichia* Eaton in North America is reviewed. Males and females of *I. clavata* Morton, *I. mazon* Ross, and *I. mexicana* Harris and Contreras-Ramos are illustrated, and a key is provided for their separation. Females of *I. mazon* and *I. mexicana* are described for the first time; the female of *I. clavata* is redescribed.

Key Words: Trichoptera, Hydroptilidae, *Ithytrichia,* taxonomy, nearctic distribution

The holarctic genus *Ithytrichia* (Eaton 1873) is a small group of microcaddisflies with six species worldwide (Marshall 1979, Morse 1993) belonging to the subfamily Hydroptilinae, tribe Orthotrichiini. Three species, *I. clavata* Morton, *I. mazon* Ross, and *I. mexicana* Harris and Contreras-Ramos, are found in North America (Morse 1993). Adults are distinguished from those of other nearctic hydroptilid genera by the presence of ocelli, a 0-3-4 tibial spur count, mesoscutellum without transverse suture, and posterodorsal margin of mesoscutellum separated from posterior margin by a narrow strap (Moulton and Stewart 1996). The laterally compressed abdomen having dorsal and ventral membranous lobes easily identifies larvae of *Ithytrichia*; the larval case is composed entirely of silk and is purse-like with a small circular anterior opening (Wiggins 1996). Morphological characters have not been discovered to distinguish the larvae to species. Before this study, only the female of *I. clavata* was known. In this paper, we describe for the first time the females of *I. mazon* and *I. mexicana.* Males of the three species are reillustrated with accompanying distributional notes. Keys for separating males and females of the three North American species are also provided.

Material examined in this study is deposited at the Arkansas State University Museum of Zoology, Jonesboro (ASUMZ), the California Academy of Sciences, San Francisco (CAS), the C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins (CSU), the Illinois Natural History Survey, Champaign (INHS), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), the Ohio Biological Survey, Columbus (OBS), the University of Minnesota, St. Paul (UM), the University of North Texas, Denton (UNT), and in the research collection of the senior author (SRM). Although most specific characters may be discerned by using a dissecting microscope (60–100×), it is necessary to view some of the female genitalic characters (e.g., spermathecal sclerite) by using a compound microscope (100–400×). Morphological terminology follows that of Marshall (1979). Length is measured from the tip of the head to the posterior tip of the forewings.

Ithytrichia clavata Morton
(Figs. 1, 4, 7)

Ithytrichia clavata Morton 1905:67.

Ross (1944) described the female of *I. clavata,* however, the discovery of the females of *I. mazon* and *I. mexicana* necessitates a redescription for comparison.

Female description.—Length 2.9–3.5 mm. 21 antennal segments. Light brown in alcohol. Sternite VI with short acute ventromesal process. Sternite VII in ventral view dome-shaped. Sternite VIII in ventral view parallel-sided, posterior margin with series of stout setae, each arising from a membranous tubercle; ventral sclerite widening posteriorly, posterior margin with broad concavity, bi-lobed, each lobe with a membranous pocket; two pairs of lateral apodemes. Segment IX bullet-shaped in ventral view; one pair of lateral apodemes. Segment X button-like with a pair of short cerci. Apodemes slender and rod-like, one pair extending from anterior end of segment X apodemes, other pair from anterior edge of segment VIII, both pairs extending to segment VI, with anterior apices gently curving mesad. Spermathecal sclerite in ventral view with anterior membranous and circular; basal one-third sclerotized on lateral margins, anterior apices angled laterad, gradually tapering posteriorly to pointed, incurved apices, middle portion of sclerotized apparatus arrowhead-shaped; posterior two-thirds widest at base, narrowing in middle to tubular apex, middle portion with lateral patches of minute spines.

Material examined.—USA: CALIFORNIA, Colusa Co., Bear Creek, 26 km E Clearlake Highlands, 28-VII-1974, P. Peterson, 6 ♂ (CAS); Lake Co., elev. 402 m, 16-IX-1949, H. P. Chandler, 1 ♂ (CAS); Napa Co., Capell Cr., 7-VI-1952, 1 ♂ (CAS); Big Canyon Creek, 13 km NE Middletown, 23-VI-1974, P. Peterson, 1 ♂ (CAS); FLORIDA, Jackson Co., Florida Caverns State Park, 4-V-1970, 2 ♂ (NMNH); ILLINOIS, Galena River, Council Hill, 26-VI-1940, Mohr and Riegel, 10 ♂ (INHS); MAINE, Ashland, 29-VII-1924, 1 ♂ (CAS); Orono, Lake Pushaw, 1-3-VIII-1966, W. W. Wirth, 3 ♂ (NMNH); Oxbow (T9R5), 22-VII-1961, A. Brower, 2 ♂ (NMNH); Allagash, 29-VII-1959, 32 ♂ (NMNH); same but, 30-VII-1959, 130 ♂ (NMNH); same but, 5-VIII-1959, 8 ♂ (NMNH); MISSOURI, Gasconade Co., Gasconade River, Held's Island Access, 28-VIII-1990, B. C. Poulton, 3 ♂ (UNT); Maries Co., Gasconade River, Island Ford Resort @ Hwy 42, 7-VIII, 1990, B. C. Poulton, 1 ♂ (UNT); same but, Paydown Access, SW Belle, 15-VII-1990, 1 ♂ (UNT); Osage Co., Gasconade River, Hwy 89 @ Dallas Ferry Access, 27-IX-1990, B. C. Poulton, 2 ♂ (UNT); PENNSYLVANIA, Presque Isle, 15-VIII-1947, 1 ♂ (CAS); Chemung River, Athens, 8-VII-1937, J. Eddleston, 23 ♂ (INHS); TEXAS, Brewster Co., county park, 8 km S Marathon, 22-VI-1994, B. Kondratieff, 5 ♂, (CSU); Edwards Co., South Llano River @ Paint Rock Springs, Hwy 337, 12-VI-1992, B. Kondratieff, 1 ♂ (CSU); Hays Co., Blanco River @ Post Rd., 14-V-1991, S. Tiemann, 3 ♂ (UNT); Palo Pinto Co., Brazos River, TX Hwy 4, 23-III-1972, Stark and Rhame, 1 ♂, 1 ♀ (NMNH), same but, 6-VI-1995, D. C. Houghton, 27 ♂, 59 ♀ (UNT); Randall Co., Prairie Dog Town Fork of Red River, Palo Duro Canyon State Park, water crossing No. 5, 12-IX-1997, S. R. Moulton and G. W. Easley, 2 ♂, 1 ♀ (SRM); WISCONISIN, Door Co., Egg Harbor, 13-VIII-1940, C. O. Mohr, 21 ♂, 15 ♀ (INHS); same but, Ephraim, WI, ?-?-1957, 1 ♀ (INHS); CANADA: MANITOBA, Lake Manitoba, 5 km W Delta, 3-VIII-1967, D. Webb, 9 ♂ (INHS); QUEBEC, Ottawa River, Quyon, 1-VIII-1976, O. S. Flint, Jr., 4 ♂, 1 ♀ (NMNH); Norway Bay, 4-VIII-1973, O. S. Flint, Jr., 4 ♂, 4 ♀ (NMNH).

Discussion.—*Ithytrichia clavata* has a holarctic distribution (Fischer 1961); it is widely distributed throughout the United States and southern Canada (Wiggins and Parker 1997). Houghton and Stewart (1998) reported on the seasonal flight periodicity

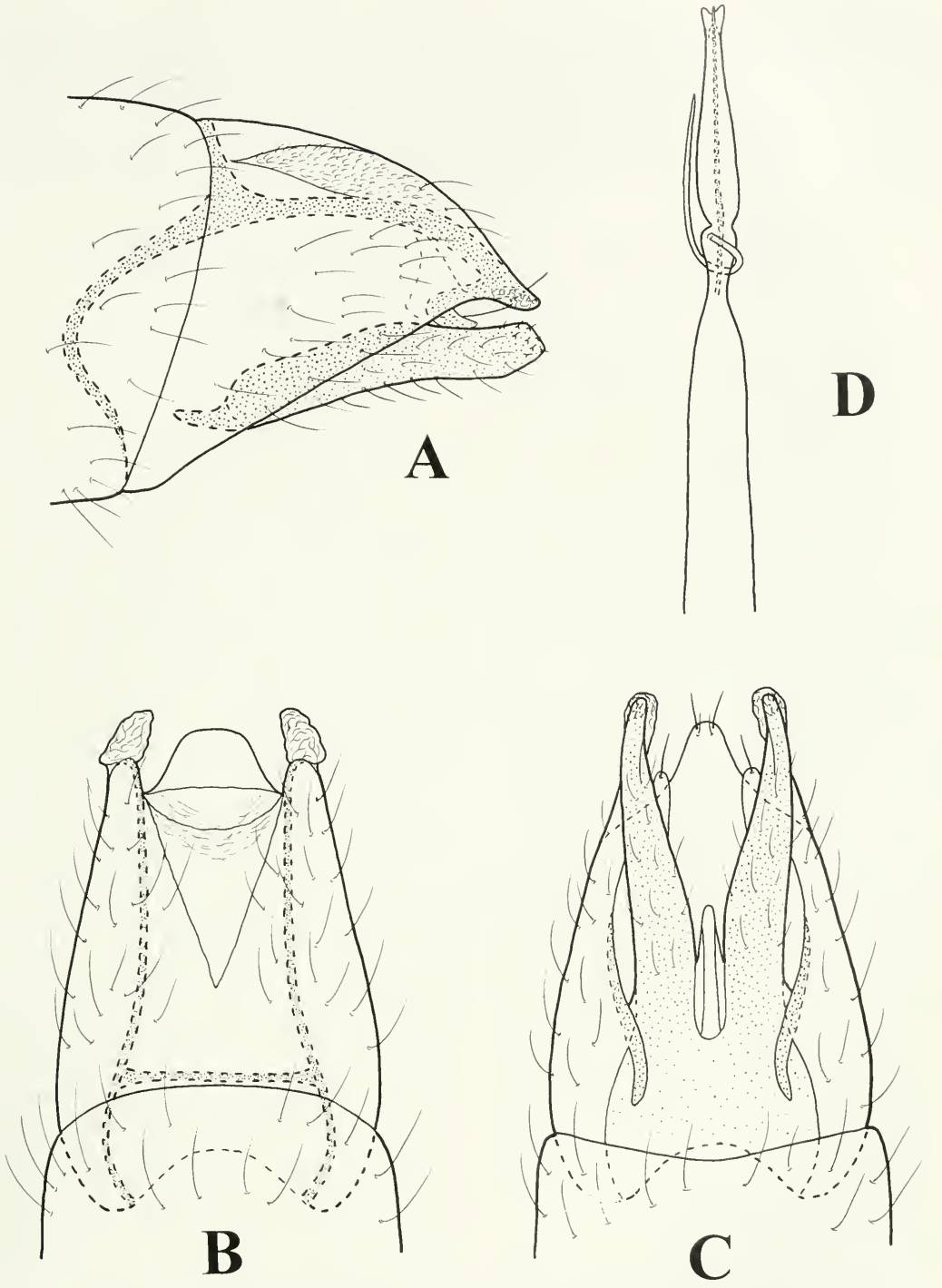


Fig. 1. *Ithytrichia clavata*, male genitalia. A, Left lateral. B, Dorsal. C, Ventral. D, Phallus.

of *I. clavata* from the Brazos River in north-central Texas. Specimens of *I. clavata* from the eastern United States determined before 1944 should be checked to ensure they are not misidentifications of *I. mazon*. We found this to be true in some of the material we examined.

Ithytrichia mazon Ross
(Figs. 2, 5, 8)

Ithytrichia mazon Ross 1944:124.

Female description.—Length 3.3–4.0 mm. 21 antennal segments. Light brown in alcohol. Sternite VI with short acute ventro-mesal process. Sternite VII in ventral view dome-shaped. Sternite VIII in ventral view parallel-sided, posterior margin with series of stout setae, each arising from a membranous tubercle; ventral sclerite widening posteriorly, apex truncate. Segment IX bullet-shaped in ventral view, apex membranous. Segment X button-like with a pair of short cerci. Apodemes slender and rod-like, one pair extending from anterior end of segment X apodemes, other pair from anterior edge of segment VIII, both pairs extending to segment VI, with anterior apices gently curving laterad. Spermathecal sclerite in ventral view with anterior a membranous funnel-shape; basal one-third sclerotized laterally and bowed, middle portion of sclerotized apparatus arrowhead-shaped; posterior two-thirds widest at base, narrowing in middle to tubular apex, middle portion with lateral patches of minute spines.

Material examined.—USA: ARKANSAS, Logan Co., Sixmile Creek, 23-V-1986, H. W. Robison, 1 ♂ (INHS); ILLINOIS, Mazon, along Mazon Creek, 16-VI-1938, B. D. Burks, holotype ♂ (INHS); Serena, Indian Creek, 16-VI-1939, B. D. Burks, 1 ♂ (INHS); OHIO, Adams Co., Hills Fork-Eagle Creek, SR 125, W West Union, OH, 27-VI-1993, B. Armitage, UV trap, 37 ♂, 52 ♀ (OBS); OKLAHOMA, Latimer Co., 10-VI-1931, R. D. Bird, 3 ♂, 3 ♀ (1 vial each sex, INHS).

Discussion.—This species appears to be restricted to small streams in the Ohio and middle Mississippi River drainages. New state records are presented here for Ohio and Oklahoma. In addition to the states listed above, *I. mazon* has also been recorded from the Salt River drainage, Spencer Co., Kentucky (Resh 1975).

Ithytrichia mexicana Harris and Contreras-Ramos
(Figs. 3, 6, 9)

Ithytrichia mexicana Harris and Contreras-Ramos 1989:176.

Female description.—Length 3.5 mm. 20 antennal segments. Brown in alcohol. Sternite VI with short acute ventro-mesal process. Sternite VII in ventral view subrectangular. Sternite VIII in ventral view parallel-sided, posterior margin with series of stout setae, each arising from a membranous tubercle; ventral sclerite with anterolateral flaps, each bearing a series of short setae, narrowing to truncate posterior margin, posterior margin with a short mesal process. Segment IX bullet-shaped in ventral view. Segment X button-like with a pair of short cerci. Apodemes slender, rod-like, extending from segment IX to VII, anterior apices straight, second pair of lateral apodemes branching from mesal pair at approximately the anterior margin of segment VIII. Spermathecal sclerite in ventral view with anterior portion forming a funnel-shaped collar constricted in middle; basal one-half sclerotized laterally with anterior apices acutely produced mesad, gradually tapering posteriorly to pointed, incurved apices, middle portion of sclerotized apparatus arrowhead-shaped; posterior one-half widest at base with lateral patches of minute spines, narrowing in middle to tubular apex, middle portion with short mesal incision; anterior and posterior portions joining with lateral membranous lobes.

Material examined.—USA: ARIZONA, Coconino Co., Oak Creek at Sterling Spring Fish Hatchery, U.S. Hwy 89A, elev. 1,829 m, 4-5-VI-1993, S. Moulton and K. Alex-

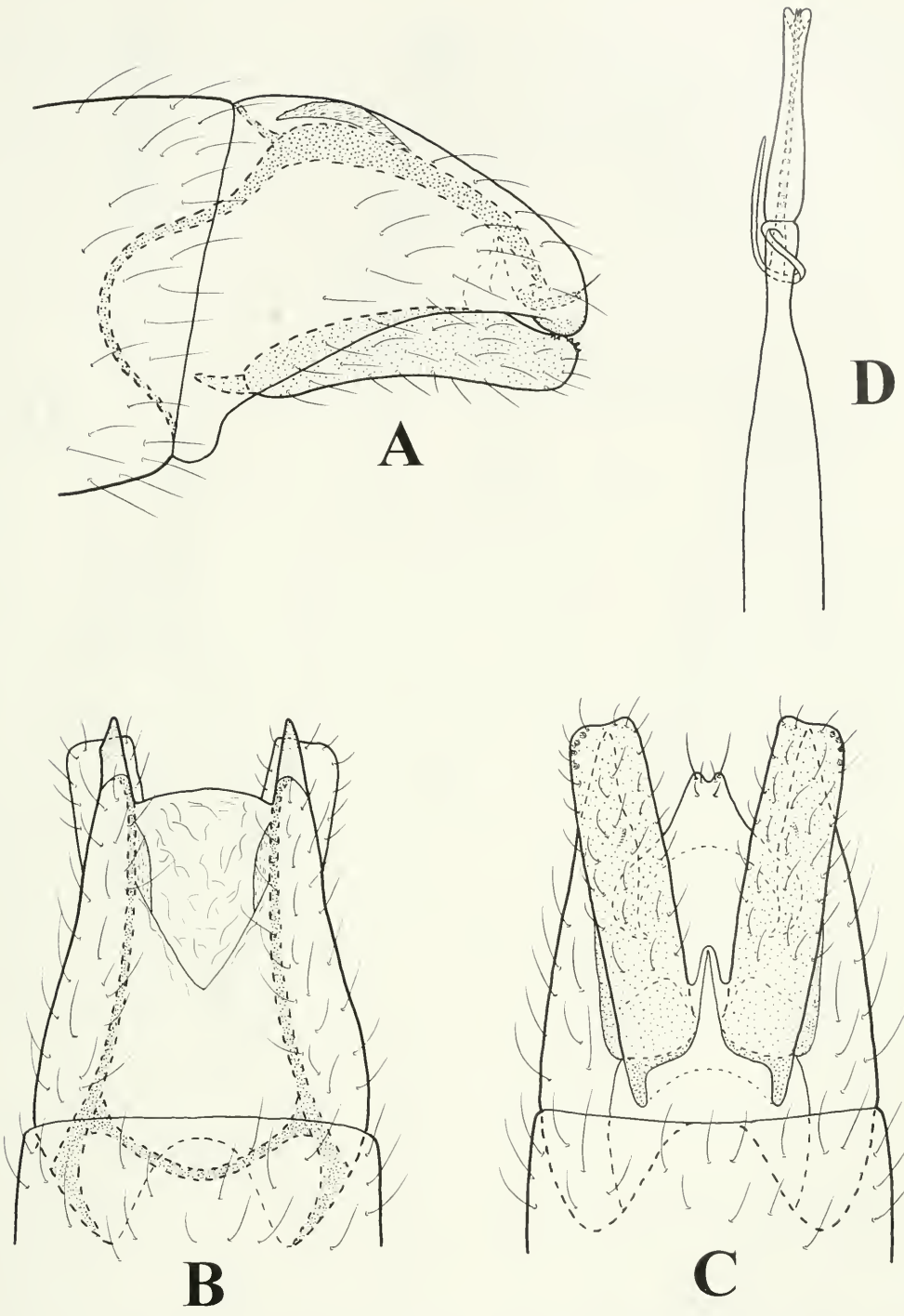


Fig. 2. *Ithytrichia mazon*, male genitalia. A, Left lateral. B, Dorsal. C, Ventral. D, Phallus.

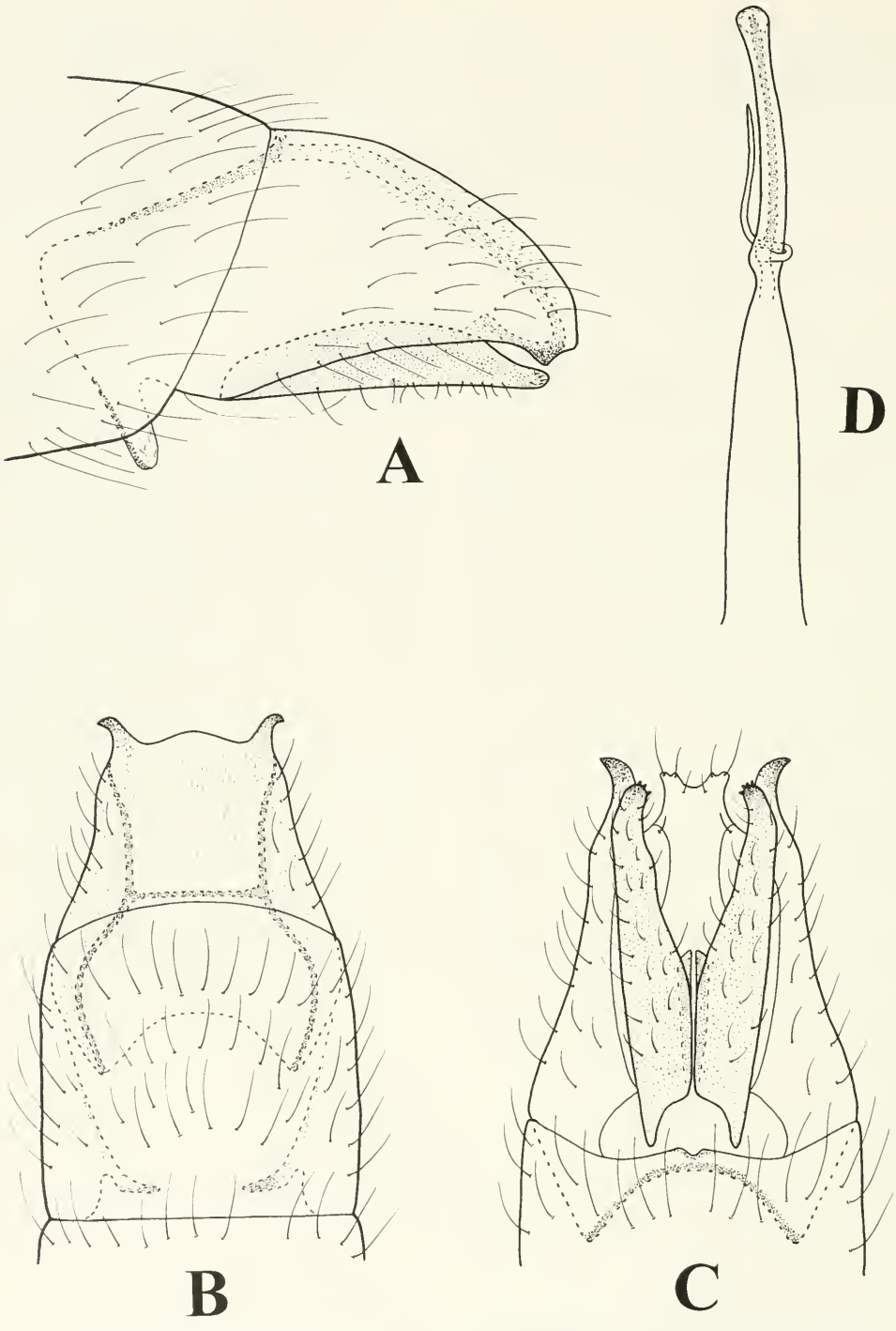
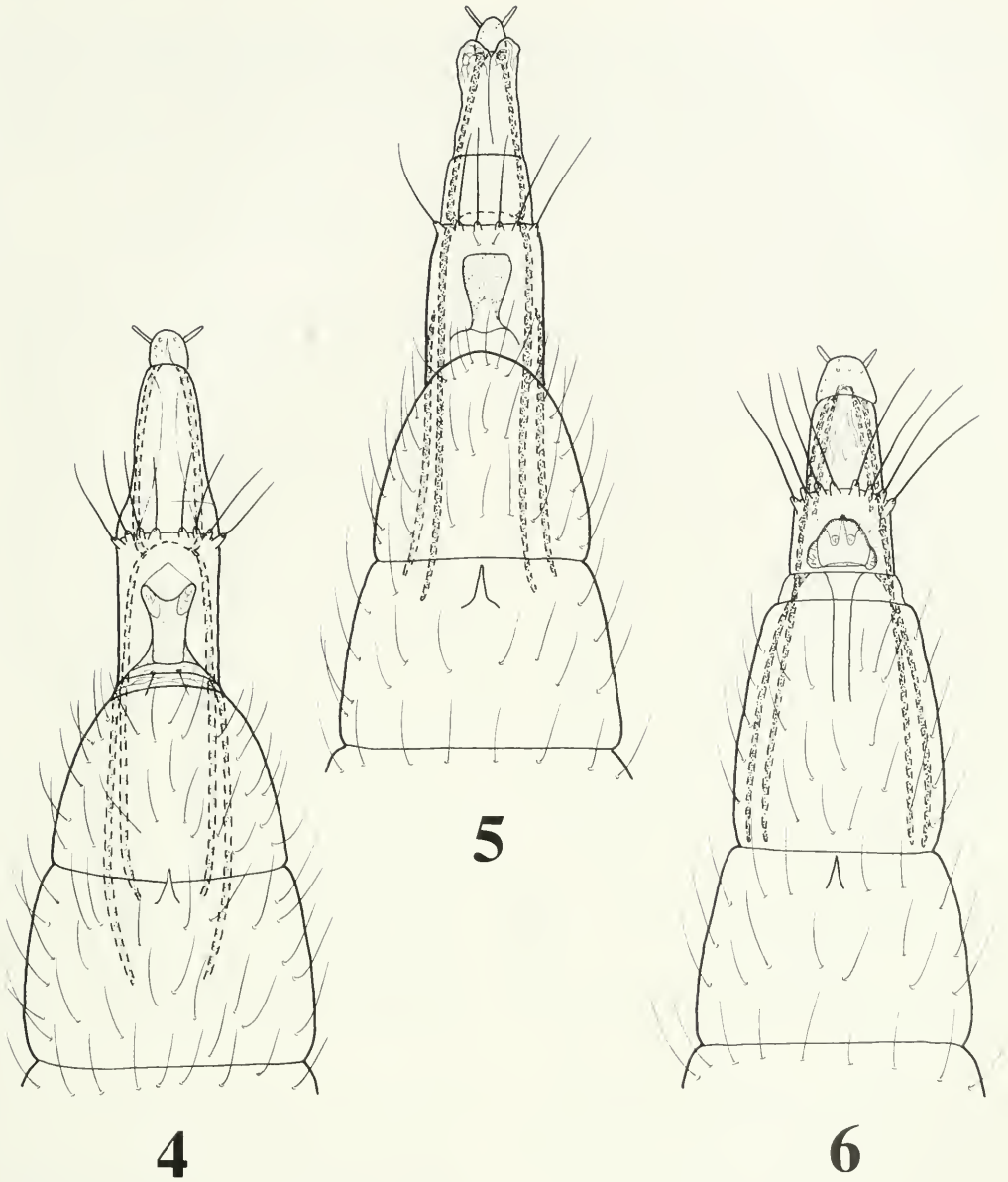


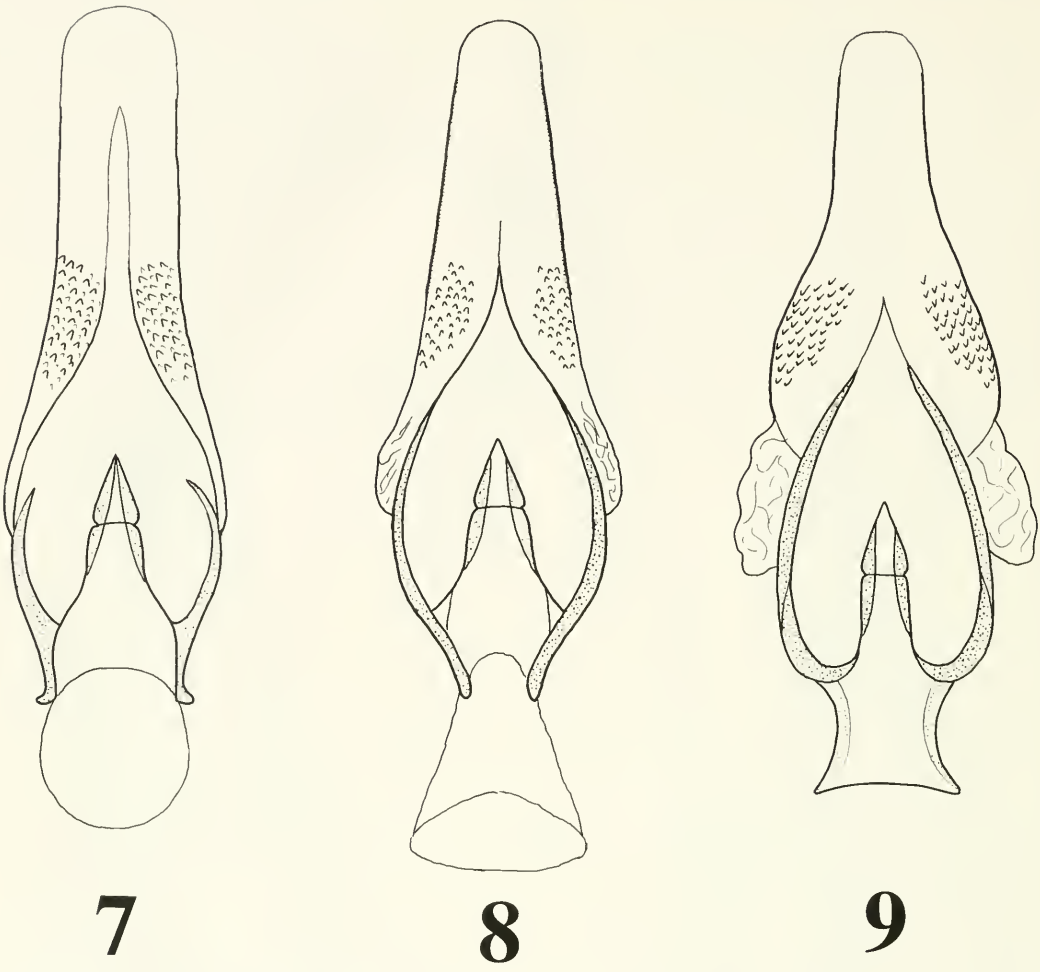
Fig. 3. *Ithytrichia mexicana*, male genitalia. A, Left lateral. B, Dorsal. C, Ventral. D, Phallus.



Figs. 4–6. *Ithytrichia* female genitalia, ventral. 4, *I. clavata*. 5, *I. mazon*. 6, *I. mexicana*.

ander, 2 ♂ (UM); NEW MEXICO, Sandoval Co., Rito de los Frijoles @ Bandelier National Monument, 10.4 km S Los Alamos, elev. 1,839 m, 2-VIII-1994, L. F. Carter, 1 ♂ (INHS), same but 1-3-VIII-1997, J. Slusark and B. Richards, UV trap, 1 ♀ (NMNH). MEXICO: TAMAULIPAS, Municipio de Gomez Farias, Rio Frio @ headwaters, La Poza Azul, 6 km S Gomez Farias, 7-VIII-1988, A. Contreras and A. Moreno, blacklight, holotype ♂ (NMNH).

Discussion.—This species was originally described by Harris and Contreras-Ramos (1989) based on a single male collected from the headwaters of the Rio Frio, Tamaulipas, Mexico. The Arizona record listed above was erroneously reported as a new Arizona state record for *I. clavata* by Moul-



Figs. 7–9. *Ithytrichia* spermathecal sclerites, ventral. 7, *I. clavata*. 8, *I. mazon*. 9, *I. mexicana*.

ton et al. (1994). *Ithytrichia mexicana* is reported herein from the United States for the first time and the species is now represented by a total of five specimens (4 males, 1 female). On the basis of known collection records, it appears to have an affinity for small cold mountain streams in the southwestern United States and northern Mexico at about 1,800 m in elevation.

Undetermined *Ithytrichia* Material

We examined several larvae and pupae in this study that could not be positively determined to species. However, speculation as to their probable identity is indicated in brackets for a few records based on distributional information.

Material examined.—ARIZONA, Gila Co., Christopher Creek, AZ 260, ca. 40 km NE Payson, elev. 1,792 m, 14-VII-1985, A. R. Brigham, 2 larvae (INHS) [*I. mexicana*]; Christopher Creek, ?-?-1985, A. Brigham, 8 larvae (INHS) [*I. mexicana*]; Lower Horton Creek, 12-VIII-1937, Tazwell, 1 larva (INHS); ARKANSAS, Randolph Co., Jane's Creek, AR Hwy 90, S Ravenden Springs, III-1985, S. R. Moulton, 1 larva (ASUMZ); MAINE, Washington Co., Narraguagus River, island, 6-VII-1973, T. Mingo, 2 pupae, 5 larvae (NMNH) [*I. clavata*];

TEXAS, Pecos River, Sheffield, 6-I-1976, J. Davis, 6 larvae (NMNH) [*I. clavata*]; WISCONSIN, Madison, Fox River, Lake Winnebago, ?-?-1954, K. M. Mackenthun, 1 larva (INHS) [*I. clavata*].

Key to the North American Species of *Ithytrichia*

1. Male (Figs. 1–3) 2
– Female (Figs. 4–6) 4
2. Inferior appendages in ventral view tapering posterad, apices rounded (Figs. 1C, 3C) 3
– Inferior appendages in ventral view rectangular, apices truncate (Fig. 2C) . . . . . *I. mazon*
3. Posterolateral margins of tergum IX sclerotized, hooked laterad (Fig. 3B); apex of subgenital plate emarginate (Fig. 3C) . . . . . *I. mexicana*
– Posterolateral margins of tergum IX rounded, not hooked (Fig. 1B); apex of subgenital plate dome-shaped (Fig. 1C) . . . . . *I. clavata*
4. Ventral sclerite of VIII gradually widening posteriorly (Figs. 4, 5); lateral sclerites of spermathecal sclerite less than one-half length of entire apparatus, ending anterolaterally in angled or rounded apices (Figs. 7, 8) 5
– Ventral sclerite of VIII narrowing posteriorly (Fig. 6); lateral sclerites of spermathecal sclerite about one-half length of entire apparatus, anterior apices curving inward to join arrowhead-shaped mesal process (Fig. 9) . . . . . *I. mexicana*
5. Ventral sclerite of VIII with concave posterior margin (Fig. 4); lateral processes of spermathecal sclerite short, anterolaterally angled outward (Fig. 7) . . . . . *I. clavata*
– Ventral sclerite of VIII with truncated posterior margin (Fig. 5); lateral processes of spermathecal sclerite elongate, rounded anteriorly (Fig. 8) . . . . . *I. mazon*

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CHECKLIST AND HOST PLANTS OF THE TREEHOPPERS (HEMIPTERA: MEMBRACIDAE) OF NORTH CAROLINA

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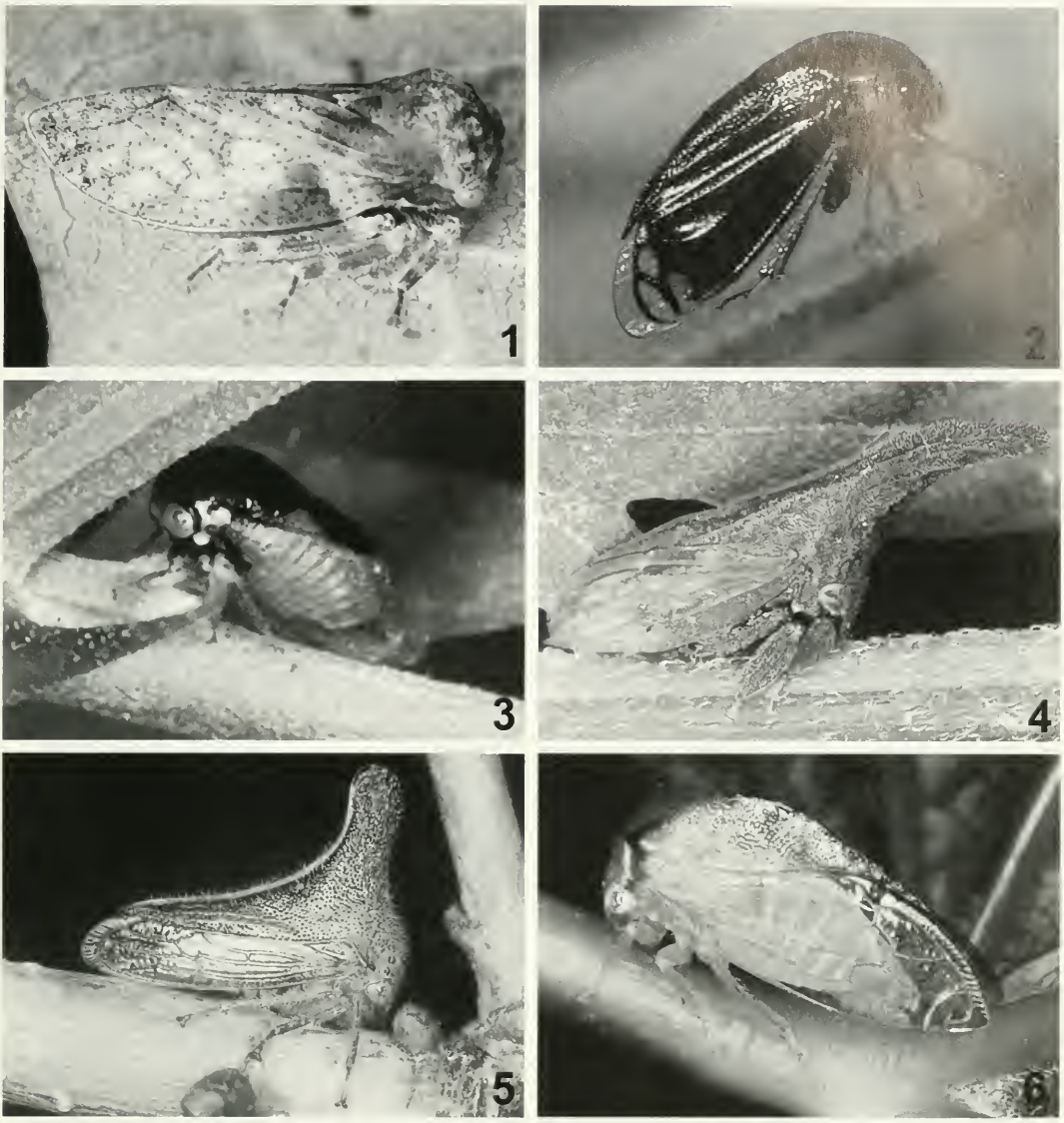
Abstract.—Based on recent collecting and an examination of museum specimens, at least 89 treehopper species (Hemiptera: Membracidae) occur in North Carolina, of which 26 species represent new state records. The presence of 13 species previously recorded from North Carolina could not be verified based on available material. Three previous North Carolina records were found to be based on misidentifications. The known distribution (by county) and host plants in North Carolina are given for each species. Photographs of representative taxa and a host plant index are included. *Stictocephala bisonia* Kopp and Yonke is reinstated as a valid name (and not a junior synonym of *Ceresa alta* Walker).

Key Words: Membracidae, treehopper, taxonomy, biogeography, insect-plant interactions

The family Membracidae (Figs. 1–10) includes more than 3,000 described treehopper species worldwide (McKamey 1998). About 260 are known to occur in temperate North America. Many of these species are restricted to the mixed hardwood forests and savannas of the eastern United States, where they exploit a variety of woody and herbaceous plants as hosts for oviposition, feeding, or both. Most North American treehopper species are univoltine, solitary, and cryptic as both immatures and adults, and, hence are seldom noticed or collected. A few species, however, are multivoltine, gregarious (Figs. 7, 8), ant-mutualistic (Figs. 8, 10), or aposematic (Fig. 7), and are therefore somewhat conspicuous. Three kinds of life cycles are common among North American treehoppers (Table 1). Many members of category III that feed and oviposit on oaks (Figs. 5, 8) are usually found as adults for only a few weeks in May or June, depending on the location within the state.

Records of North Carolina treehoppers were summarized by Metcalf (1915), Brimley (1938, 1942), Wray (1950, 1967), Metcalf and Wade (1965), and Kopp and Yonke (1973a–c, 1974: distribution maps). Kopp and Yonke's series provided keys to many species in eastern North America. Deitz et al. (1976), McGiffen and Neunzig (1985), and Hargrove (1986) gave further records of North Carolina treehoppers associated with soybeans, grapes, and black locust, respectively.

The objectives of the present work were to document the species richness of North Carolina treehoppers, summarize the known distributions (Fig. 11: county map) and host plant associations within the state, and provide an up-to-date checklist following current nomenclature. Although host records for numerous species have been published (e.g., Funkhouser 1917; Ball 1931; Kopp and Yonke 1973a–c, 1974), the extent to



Figs. 1–6. Representative treehoppers of North Carolina. 1, *Microcentrus caryae*. 2, *Acutalis tartarea*. 3, *Micrutalis calva*. 4, *Campylenchia latipes*. 5, *Glossonotus univittatus*. 6, *Stictocephala militaris*.

which host associations vary geographically is poorly documented and most published records have not been verified through rearing of immatures.

Materials and Methods

The species records below are based on specimens in the following collections: the North Carolina State University Insect Collection, Raleigh [NCSU: includes recent material from the authors]; Mark J. Rothschild Collection, % Maryland Department of Agriculture, Salisbury [MJRC]; Florida State Collection of Arthropods, Gainesville [FSCA]; North Carolina Department of Agriculture, Raleigh [NCDA]; and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. [USNM]. C. S. Brimley's historically important material is housed at the collections of NCDA (specimens and card files) and NCSU (specimens).

Figs. 7–10. Representative treehoppers of North Carolina (continued). 7, *Platycotis vittata,* aggregation of teneral adults. 8, *Vanduzea arquata,* aggregation of adults and nymphs attended by ants. 9, *Ophiderma evelynae:* left, female (green), right, male (brown). 10, *Entylia carinata* (left) and *Publilia concava* (right, attended by ant).

Table 1. Three major kinds of life cycles in treehoppers of eastern North America (modified from Kopp and Yonke 1973a).

Category: Taxa	Overwintering	Development	Generations Per Year
I: Polyglyptini, *Platycotis vittata*, probably *Campylenchia latipes*, some *Vanduzea* and some Ceresini	adults overwinter in litter	nymphs feed and develop on herbaceous or woody host plants	2 (most are bivoltine)
II: Acutalini, most Ceresini, some *Micrutalis*	eggs overwinter under bark in young twigs of woody hosts	nymphs feed and develop on herbaceous host plants (many females require preoviposition period before laying eggs)	1 (univoltine)
III: Smiliini, *Microcentrus* spp., *Enchenopa binotata* complex, some *Micrutalis*	eggs overwinter under bark in young twigs of woody hosts	nymphs feed and develop on same woody hosts used for oviposition	1 (most are univoltine)

Records are based on adult specimens except as noted. Among species of Ceresini, males are generally required for positive identification (Kopp and Yonke 1979); consequently, females without associated males often could not be identified. Each entry includes a list of counties in North Carolina from which the species has been recorded, the seasonal distribution (earliest and latest calendar date of collection of adults), and North Carolina host records. A few specimens bore labels indicating a locality situated on the border of two or three counties; these were considered to occur in all of the counties involved.

Except as noted, only North Carolina host associations based on specimens examined are reported here. Hosts marked with an asterisk (*) are those from which both nymphs and adults have been collected. Other plants listed are those from which only adults have been collected, so some may not be true hosts. Botanical nomenclature follows Kartesz (1994), Liberty Hyde Bailey Hortorium (1976), and Radford et al. (1968). To conserve space, botanical common names and the authors of plant scientific names are given only in the alphabetical host index.

To facilitate comparisons with *The Insects of North Carolina* (Brimley 1938, 1942, Wray 1950, 1967), and *The Treehoppers of Missouri* (Kopp and Yonke 1973a–c, 1974), names from those works that differ from current nomenclature are given for each entry in square brackets (occasionally with other notes on synonymy). For additional synonymy, see Fascicle 1, Membracidae, and its supplements, in the *General Catalogue of the Hemiptera* (Funkhouser 1927, Metcalf and Wade 1965, McKamey 1998) and the associated bibliographies (Metcalf and Wade 1963, Deitz and Kopp 1987, Deitz 1989).

For convenience, the checklist is arranged alphabetically by genus and species. Table 2 summarizes the placement of the included genera into tribes and subfamilies.

Results

Recent collecting in North Carolina yielded numerous new state, county, and host records. Figure 11 indicates the number of treehopper species recorded for each of North Carolina's 100 counties. The higher species richness recorded near Raleigh (Wake County, 68 species), Asheville (Buncombe County, 39 species), Boone (Watauga county, 30 species), and Charlotte

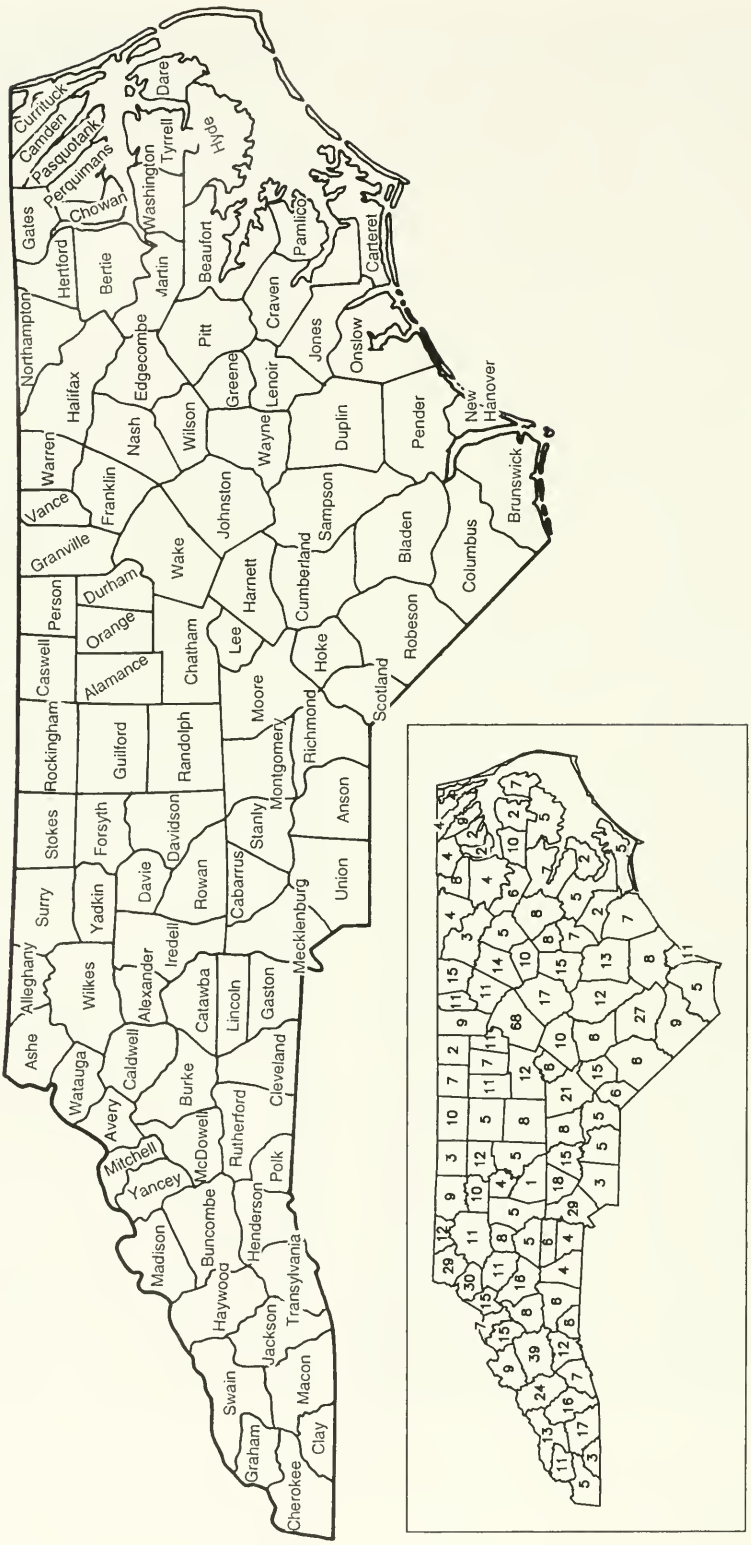


Fig. 11. North Carolina map with number of treehopper species recorded from each county.

Table 2. Summary of the classification of North Carolina Membracidae (based on Deitz 1975, Kopp and Yonke 1979, and Deitz and Dietrich 1993).

Subfamily Stegaspidinae:
Tribe Microcentrini: *Microcentrus* Stål 1869 (Fig. 1).
Subfamily Membracinae:
Tribe Hoplophorionini: *Playcotis* Stål 1869 (Fig. 7).
Tribe Membracini: *Tylopelta* Fowler 1894; *Campylenchia* Stål 1869 (Fig. 4); *Enchenopa* Amyot & Serville 1843.
Subfamily Smiliinae:
Tribe Acutalini: *Acutalis* Fairmaire 1846 (Fig. 2).
Tribe Micrutalini: *Micrutalis* Fowler 1895 (Fig. 3).
Tribe Ceresini: *Hadrophallus* Kopp and Yonke 1979; *Stictolobus* Metcalf 1916; *Tortistilus* Caldwell 1949; *Stictocephala* Stål 1869 (Fig. 6); *Spissistilus* Caldwell 1949.
Tribe Amastrini: *Vanduzea* Goding 1892 (Fig. 8).
Tribe Smiliini: *Archasia* Stål 1867; *Carynota* Fitch 1851; *Glossonotus* Butler 1877 (Fig. 5); *Heliria* Stål 1867; *Telamona* Fitch 1851; *Thelia* Amyot and Serville 1843; *Atymna* Stål 1867; *Cyrtolobus* Goding 1892; *Ophiderma* Fairmaire 1846 (Fig. 9); *Smilia* Germar 1833; *Xantholobus* Van Duzee 1908.
Tribe Polyglyptini: *Publilia* Stål 1866 (Fig. 10, right); *Entylia* Germar 1833 (Fig. 10, left).

(Mecklenburg County, 29 species) reflects greater collecting effort in those areas.

With at least 89 species, North Carolina ranks third among the few states for which treehopper checklists have been published. New York ranks first (100 currently recognized species: Leonard 1928) and Ohio second (93 currently recognized species, including two presumed present based on records in neighboring states: Osborn 1940), but dubious identifications may have inflated the accuracy of counts for those states. Among treehoppers, males, females, or both may be polymorphic with respect to pronotal shape and coloration (Figs. 7, 9). Frequently, previous workers incorrectly identified a single polymorphic species as two or more distinct species.

Thirteen species previously reported from North Carolina whose occurrence in the state we could not verify and three previously misidentified species—*Hadrophallus constans* (Walker), *Spissistilus uniformis* (Fairmaire), and *Telamona concava* Fitch, are included below in square brackets.

Five additional species reported from adjacent states may eventually be found in North Carolina, but are not included in the checklist: *Palonica pyramidata* (Uhler), *Stictocephala albescens* (Van Duzee), and *Thelia uhleri* Stål, all reported from Virginia (Kopp and Yonke 1973b, 1974: distribution maps); *Helonica excelsa* (Fairmaire), reported from South Carolina (Kopp and Yonke 1974: map); and *Telamona compacta* Ball (specimen [USNM] from Rocky Bottom, South Carolina [<10 miles from Transylvania County, North Carolina]).

Table 3. Comparison of treehopper diversity in the world, the Nearctic Region, and North Carolina (based on McKamey 1998 and the present work).

Geographic Area	Species	Genera	Tribes	Subfamilies
World	3,177	397	49	12
Nearctic Region	258	62	13	6
North Carolina	89	26	9	3

Table 3 shows the species richness of North Carolina's treehopper fauna compared to the Nearctic Region and the world. Especially well represented in North Carolina are the genera *Cyrtolobus* (21 species), *Telamona* (10), *Ophiderma* (7), and *Heliria* (6). All species recorded are native to North Carolina and nearly all are endemic to the eastern U.S.

North Carolina treehoppers have been collected on at least 45 plant genera in 19 families, including 12 genera of Asteraceae,

9 of Fabaceae, and 3 of Fagaceae. Moreover, 39 species (43 percent of the state's membracid fauna) may be found on oaks (Fagaceae), with 16 species of *Quercus* listed below as hosts.

Checklist of North Carolina Membracidae

Acutalis tartarea (Say 1830) [in part as *Acutalis tartarea* var. *semicrema* (Say 1830) in Brimley 1938]. Fig. 2. Counties: Alamance, Alexander, Anson, Ashe, Beaufort, Bladen, Buncombe, Burke, Cabarrus, Caldwell, Carteret, Chatham, Davidson, Duplin, Edgecombe, Forsyth, Granville, Haywood, Henderson, Hyde, Jackson, Johnston, Mecklenburg, Nash, Onslow, Orange, Pamlico, Pasquotank, Person, Polk, Rutherford, Stanly, Surry, Tyrrell, Wake, Warren, Washington, Watauga, Wayne, Wilkes, Wilson. Seasonal distribution: 24 May–23 November. Host associations: *Ambrosia artemisiifolia, Arundinaria* sp., *Bidens coronata, Eupatorium capillifolium, Helianthus* sp., *Solidago* sp.

Archasia auriculata (Fitch 1851) [as *A. galeata* (Fabricius 1803), a preoccupied name, in Brimley 1938]. Counties: Bladen, Buncombe, Columbus, Moore, Wake. Seasonal distribution: 9 May–27 August. Host associations: *Quercus nigra, Q. velutina**.

Archasia belfragei Stål 1869. Counties: Bladen, Buncombe, Columbus, Henderson, Macon, Wake. Seasonal distribution: 12 May–11 September. Host associations: *Quercus alba**, *Q. phellos*. Notes: Brimley's (1938) record of *A. belfragei* from Southern Pines (Moore County, June), actually represents a specimen (NCDA) of *A. auriculata*.

Atymna castaneae (Fitch 1851) [as *Cyrtolobus castaneus* (Fitch) in Brimley 1938]. Counties: Ashe, Bladen, Buncombe, Burke, Graham, Haywood, Jackson, Sampson, Surry, Swain, Watauga, Yancey. Seasonal distribution: 23 May–31 August. Host associations: *Castanea dentata**, *C. pumila**.

[*Atymna inornata* (Say 1830)]. Records of this species in North Carolina (Metcalf 1915, Van Duzee 1917, Brimley 1938 [as *Cyrtolobus inornata*]) were not verified by the present authors.

Atymna querci (Fitch 1851). Counties: Alleghany, Ashe, Buncombe, Cabarrus, Cleveland, Duplin, Forsyth, Haywood, Macon, Martin, Nash, Orange, Vance, Wake, Warren, Washington, Watauga, Wayne, Yadkin. Seasonal distribution: 14 April–8 September. Host associations: *Quercus alba**, *Q. stellata**, *Vitis rotundifolia*.

Campylenchia latipes (Say 1824). Fig. 4. Counties: Alamance, Alexander, Alleghany, Ashe, Avery, Bladen, Brunswick, Buncombe, Burke, Cabarrus, Caldwell, Chatham, Cleveland, Davidson, Davie, Duplin, Durham, Forsyth, Graham, Granville, Guilford, Halifax, Haywood, Johnston, Jones, Macon, Madison, Martin, McDowell, Mecklenburg, Mitchell, Montgomery, Moore, New Hanover, Onslow, Orange, Pender, Polk, Rutherford, Sampson, Scotland, Stanly, Swain, Transylvania, Wake, Warren, Washington, Watauga, Wayne, Wilkes, Yadkin. Seasonal distribution: [? 4 May (NCSU)], 3 June–21 November. Host associations: *Medicago sativa, Solidago* sp.

Carynota marmorata (Say 1830). Counties: Haywood, Henderson, Jackson, Moore, Stanly, Wake, Watauga. Seasonal distribution: 6 June–30 July. Host associations: *Betula* sp.

Carynota mera (Say 1830). Counties: Bladen, Currituck, Hyde, Mecklenburg, New Hanover, Pitt, Wake. Seasonal distribution: [18 May, nymphs], 21 May–late October. Host associations: *Carya illinoinensis, C.* sp*.

Cyrtolobus arcuatus (Emmons 1854). Counties: Greene, Harnett, Hertford, Wake. Seasonal distribution: 24 April–12 May. Host associations: *Quercus falcata**, *Q. phellos*.

Cyrtolobus auroreus Woodruff 1924. NEW STATE RECORD. Counties: Ashe, Duplin, Guilford, Macon, Mecklenburg, Wake, Wayne. Seasonal distribution: 23 April–19–20 June. Host associations: *Quercus alba**, *Q. prinus*.

Cyrtolobus celsus Van Duzee 1917 [as *C. celsis* (sic) in Brimley 1938]. Counties: Moore. Seasonal distribution: 22 May. Host associations: no data for North Carolina.

Cyrtolobus clarus Woodruff 1924. NEW STATE RECORD. Counties: Wake. Seasonal distribution: 4–25 May. Host associations: *Quercus palustris**, *Q. phellos**.

[*Cyrtolobus discoidalis* (Emmons 1854)]. Brimley's (1938) record of this species in North Carolina (Balsam, Jackson County) could not be verified, but may be the basis for Kopp and Yonke's (1973c: map) record.

Cyrtolobus dixianus Woodruff 1924. NEW STATE RECORD. Counties: Cabarrus, Duplin, Franklin, Wake. Seasonal distribution: 26 April–26 May. Host associations: *Quercus alba, Q. falcata, Q. palustris, Q. stellata**.

Cyrtolobus fenestratus (Fitch 1851). Counties: Bladen, Dare, Edgecombe, Forsyth, Greene, Hertford, Hoke, Johnston, Lenoir, Nash, Pasquotank, Robeson, Rockingham, Wake, Washington, Wilson. Seasonal distribution: [15 April, nymph], 24 April–19 May. Host associations: *Quercus falcata**, *Q. laevis, Q. margarettiae, Q. marilandica**, *Q. nigra**, *Q. palustris, Q. phellos**, *Q. rubra**, *Q. velutina, Q. virginiana*. Notes: Brimley's (1938) June record of *C. fenestratus* from Blowing Rock (Watauga County) was not verified by the present authors, while his July record from Blowing Rock may represent a specimen (NCDA) of *C. puritanus* Woodruff.

Cyrtolobus flavolatus Woodruff 1924. NEW STATE RECORD. Counties: Buncombe, Vance, Wake. Seasonal distribution: 18 May–18 June. Host associations: no data for North Carolina.

Cyrtolobus fuliginosus (Emmons 1854). Counties: Cabarrus, Franklin, Greene, Harnett, Hertford, Johnston, Lenoir, Martin, Mecklenburg, Pasquotank, Randolph, Wake, Warren, Washington, Wayne. Seasonal distribution: 23 April–26 May. Host associations: *Quercus coccinea, Q. falcata**, *Q. palustris, Q. phellos, Q. stellata, Q. velutina**.

Cyrtolobus funkhouseri Woodruff 1924. NEW STATE RECORD. Counties: Mecklenburg, Stokes, Wake, Wilkes, Yadkin. Seasonal distribution: 13 May–11 June. Host associations: *Quercus palustris*.

Cyrtolobus fuscipennis Van Duzee 1908. Counties: Ashe, Buncombe, Burke, Jackson, Macon, Mecklenburg, Wake. Seasonal distribution: 24 April–22 July. Host associations: *Quercus alba**, *Q. nigra*.

Cyrtolobus griseus Van Duzee 1908. NEW STATE RECORD. Counties: Ashe, Burke, Montgomery, Vance, Wake. Seasonal distribution: 29 April–6 July. Host associations: *Quercus alba, Q. stellata*.

Cyrtolobus inermis (Emmons 1854). NEW STATE RECORD. Counties: Bladen, Hoke, Rutherford, Wake. Seasonal distribution: 3 May–10 June. Host associations: *Quercus falcata**, *Q. marilandica**, *Q. stellata*.

Cyrtolobus maculifrontis (Emmons 1854). Counties: Ashe, Bladen, Duplin, Granville, Vance, Wake, Watauga, Wayne. Seasonal distribution: [? March (NCSU)], 23 April–27 June. Host associations: *Quercus alba**, *Q. falcata*.

Cyrtolobus ovatus Van Duzee 1908. Counties: Bladen, Hoke, Johnston, Moore, Richmond, Sampson, Wake. Seasonal distribution: 7 May–28 June. Host associations: *Quercus laevis**, *Q. marilandica**.

Cyrtolobus pallidifrontis (Emmons 1854). NEW STATE RECORD. Counties: Buncombe, Currituck, Wake, Warren, Watauga. Seasonal distribution: 29 April–26

July. Host associations: *Quercus alba, Q. stellata**.

Cyrtolobus parvulus Woodruff 1924. NEW STATE RECORD. Counties: Bladen, Moore, Richmond. Seasonal distribution: 23 May–17 June. Host associations: no data for North Carolina. Notes: Hosts reported elsewhere include two species of *Quercus* (Kopp and Yonke 1973c).

Cyrtolobus pulchellus Woodruff 1924. NEW STATE RECORD. Counties: Ashe. Seasonal distribution: 19–20 June. Host associations: *Quercus rubra.*

Cyrtolobus puritanus Woodruff 1924. Counties: Buncombe, Wake, Watauga, Yancey [as "Black Mountains," which is on the Buncombe–Yancey border (USNM)]. Seasonal distribution: 26 May–20 July. Host associations: no data for North Carolina. Notes: Brimley's (1938) record of *C. puritanus* from Lake Toxoway (Transylvania Co.) was not verified by the present authors. Hosts reported elsewhere include five species of *Quercus* (Kopp and Yonke 1973c).

[*Cyrtolobus sculptus* (Fairmaire 1846)]. Records of *C. sculptus* in North Carolina (Goding 1893, Van Duzee 1917, Brimley 1938) were not verified by the present authors.

Cyrtolobus togatus Woodruff 1924. NEW STATE RECORD. Counties: Buncombe, Cabarrus, Durham, Franklin, Harnett, Mecklenburg, Nash, Rockingham, Vance, Wake, Yadkin. Seasonal distribution: 23 April–23–30 June. Host associations: *Quercus nigra**, *Q. phellos**, *Q. stellata.*

Cyrtolobus tuberosus (Fairmaire 1846). Counties: Bladen, Cabarrus, Camden, Caswell, Columbus, Craven, Franklin, Hertford, Hoke, Lenoir, Mecklenburg, Montgomery, Nash, Northampton, Robeson, Rockingham, Wake, Warren, Wayne, Wilson. Seasonal distribution: 16 April–1 June. Host associations: *Quercus alba**, *Q. margarettiae, Q. marilandica, Q. nigra, Q. prinus, Q. rubra, Q. stellata, Q. virginiana.*

Cyrtolobus vau (Say 1830). Counties: Alleghany, Ashe, Avery, Buncombe, Caswell, Columbus, Duplin, Franklin, Haywood, Henderson, Jackson, Macon, Mecklenburg, Moore, Rockingham, Transylvania, Vance, Wake, Yancey. Seasonal distribution: late March–5 September. Host associations: *Quercus alba**, *Q. prinus, Q. stellata.*

Enchenopa binotata (Say 1824) complex (see Notes, below, for discussion of the complex). Counties: Alamance, Alleghany, Ashe, Buncombe, Carteret, Chatham, Gates, Graham, Guilford, Haywood, Iredell, Macon, Madison, McDowell, Moore, New Hanover, Richmond, Sampson, Stanly, Transylvania, Wake, Yancey. Seasonal distribution: [1 May, nymph], 15 May–3 October. Host associations: *Carya* sp., *Cercis canadensis**, *Juglans nigra**, *Liriodendron tulipifera, Robinia pseudoacacia**, *Viburnum prunifolium**. Notes: The *Enchenopa binotata* complex is thought to include nine biologically distinct North American species, each of which is associated with a different genus or species of deciduous woody host plant: (1) *Carya* spp., (2) *Celastris scandens,* (3) *Cercis canadensis,* (4) *Juglans cinerea,* (5) *J. nigra,* (6) *Liriodendron tulipifera,* (7) *Ptelea trifoliata,* (8) *Robinia pseudoacacia,* and (9) *Viburnum* spp. (Pratt and Wood 1992, 1993). Three published names are currently available for species within this complex, but the corresponding original descriptions lack host plant data as well as morphological criteria useful for distinguishing either the nymphs or adults from other species in the complex (Pratt and Wood 1992). Pratt and Wood (1992) described the fifth instar nymphs of species in the complex and provided a key for their identification, but did not attempt to resolve the nomenclatural problems.

Based on host data, specimens examined from North Carolina appear to represent five of the nine species in the complex:

*Cercis canadensis**: Buncombe and Wake Counties (10 June–5 July).

*Juglans nigra**: Ashe and Sampson County ([23 May, nymph] 5 July).

Liriodendron tulipifera: Chatham County (2 July).

*Robinia pseudoacacia**: Macon County (5 August).

*Viburnum prunifolium**: Wake County (27 May).

Entylia carinata (Forster 1771) [in part as *E. concisa* Walker 1851, and as *E. sinuata* (Fabricius 1798) in Brimley 1938; as *E. bactriana* Germar 1835, in Kopp and Yonke 1973b; *E. carinata* (Forster) in Remes-Lenicov 1973]. Fig. 10 (left). Counties: Alamance, Alexander, Alleghany, Anson, Ashe, Avery, Beaufort, Bertie, Bladen, Buncombe, Burke, Cabarrus, Caldwell, Camden, Catawba, Chatham, Cherokee, Clay, Cleveland, Cumberland, Dare, Davidson, Davie, Duplin, Durham, Edgecombe, Gaston, Gates, Graham, Granville, Harnett, Haywood, Henderson, Hertford, Hoke, Hyde, Iredell, Jackson, Johnston, Lincoln, Macon, Madison, McDowell, Mecklenburg, Montgomery, Moore, Nash, New Hanover, Onslow, Orange, Pasquotank, Perquimans, Pitt, Polk, Rockingham, Sampson, Scotland, Stanly, Surry, Swain, Transylvania, Vance, Wake, Warren, Washington, Watauga, Wayne, Yadkin, Yancey. Seasonal distribution: 13 March–19 December. Host associations: *Ambrosia artemisiifolia**, *Ambrosia* sp., *Aster* sp., *Bidens bipinnata, B. coronata, B.* sp., *Conyza canadensis* (as *Erigeron canadensis*), *Dahlia* sp., *Erechtites hieraciifolia**, *Erigeron* sp., *Eupatorium capillifolium, E. pilosum, E.* sp., *Glycine max, Helianthus annuus, H. tuberosus**, *H.* sp., *Quercus palustris, Silphium* sp., *Solanum tuberosum, Solidago* sp., *Verbesina alternifolia* (as *Actinomeris alternifolia*), *Vitis rotundifolia, V.* sp. Notes: Deitz et al. (1976) reported an *Entylia* from *Glycine max* in Columbus Co., however, the voucher material could not be located for the present study. Also, Brimley's (1938) material from Hendersonville (Henderson County) and Willard (Pender County) could not be located and his specimen (NCDA) from "Spruce" is actually labelled "Sunburst" (Haywood County).

Glossonotus acuminatus (Fabricius 1775). Counties: Duplin, Wake. Seasonal distribution: 6 May–14 June. Host associations: *Quercus falcata**.

Glossonotus turriculatus (Emmons 1854). Counties: Buncombe-Yancey [as "Black Mountains," which is on the border of these counties (USNM)]. Seasonal distribution: 15–20 June. Host associations: no data for North Carolina. Notes: Hosts reported elsewhere include *Crataegus* and *Quercus* (Kopp and Yonke 1974).

Glossonotus univittatus (Harris 1841). Fig. 5. Counties: Bladen, Burke, Mecklenburg, Rockingham. Seasonal distribution: 16 May–4 August. Host associations: *Quercus alba, Q. rubra.*

Hadrophallus borealis (Fairmaire 1846) [as *Ceresa borealis* Fairmaire in Brimley 1938; as *Spissistilus borealis* (Fairmaire) in Kopp and Yonke 1973b]. Counties: Buncombe, Stanly, Swain, Wake, Watauga. Seasonal distribution: 3 June–29 August. Host associations: no data for North Carolina. Notes: One female specimen from Waynesville, Haywood County, 14 Sept., probably *H. borealis*-was formerly misidentified as *Ceresa constans* (Walker) by Z.P. Metcalf (NCDA). Hosts reported elsewhere include species in several plant families (Kopp and Yonke 1973b).

[*Hadrophallus constans* (Walker 1851), misidentification]. Brimley's (1938) records of *Ceresa constans* (Walker) refer to *H. borealis* (Raleigh [Wake County], Waynesville [Haywood County]), *Stictocephala militaris* (Havelock), or *S. brevitylus* (Newton); Kopp and Yonke's (1973b: map) North Carolina record of this species (as *S. constans*) was probably based on Brimley's publication.

Heliria cornutula Ball 1925. NEW STATE RECORD. Counties: Bladen, Mecklenburg, Randolph, Wake. Seasonal distribution: 5 July–15 November. Host associations: no data for North Carolina.

Heliria cristata (Fairmaire 1846). Counties: [as "Eastern N.C." on data label (NCSU)]. Seasonal distribution: mid July. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1974) reported *Quercus macrocarpa* Michx.

Heliria gemma Ball 1925. NEW STATE RECORD. Counties: Graham. Seasonal distribution: 1 September. Host associations: no data for North Carolina.

Heliria gibberata Ball 1925. NEW STATE RECORD. Counties: Burke, Wake. Seasonal distribution: 23 May–late June. Host associations: no data for North Carolina. Notes: Elsewhere, Ball (1931) recorded *Celtis occidentalis* L. as a host.

[*Heliria mexicana* Stål 1869]. Records of *H. mexicana* in North Carolina (Ball 1931, Brimley 1938) were not verified by the present authors.

Heliria molaris (Butler 1877). Counties: Wake, Watauga. Seasonal distribution: August. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1974) reported *Quercus* and *Populus* as hosts.

Heliria scalaris (Fairmaire 1846). Counties: Wake. Seasonal distribution: 21 June. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1974) reported *Crateagus* as a host.

Microcentrus caryae (Fitch 1851). Fig. 1. Counties: Buncombe, Forsyth, Haywood, Martin, Pitt, Sampson, Wake. Seasonal distribution: [7 May, nymph], 25 June–4 December. Host associations: *Carya illinoinensis**, *Carya* sp.

Microcentrus perditus (Amyot and Serville 1843). Counties: Moore, Stokes, Wake. Seasonal distribution: 20 May–20 October. Host associations: *Carya illinoinensis.*

Micrutalis calva (Say 1830) [in part as *Micrutalis calva* var. *illinoiensis* (Goding 1893) in Brimley 1938]. Fig. 3. Counties: Alamance, Alexander, Alleghany, Avery, Bertie, Bladen, Brunswick, Buncombe, Cabarrus, Caswell, Chatham, Cherokee, Columbus, Cumberland, Dare, Davidson, Davie, Duplin, Durham, Forsyth, Graham, Granville, Guilford, Haywood, Hoke, Jackson, Johnston, Lincoln, Mecklenburg, Mitchell, Moore, New Hanover, Onslow, Person, Richmond, Rutherford, Scotland, Stanly, Surry, Swain, Wake, Warren, Wayne, Wilkes. Seasonal distribution: late April–2 November. Host associations: *Conyza canadensis, Erigeron annuus, Gleditsia triacanthos**, *Glycine max, Robinia pseudoacacia, Salix nigra, Solidago* sp., *Vitis rotundifolia, V.* sp. 'French hybrid'. Notes: Brimley's (1938) records from Tin City and Willard (Pender County) were not verified by the present authors.

Micrutalis dorsalis (Fitch 1851). Counties: Alleghany, Burke, Caldwell, Haywood, Swain, Watauga, Yancey. Seasonal distribution: 11 July–21 August. Host associations: no data for North Carolina.

Micrutalis malleifera Fowler 1895. NEW STATE RECORD. Counties: Dare. Seasonal distribution: 14 June. Host associations: *Physalis* sp. Notes: Mead (1986) reviewed information on this treehopper, the only known vector of pseudo-curly top virus (a minor disease of tomatoes).

Ophiderma definita Woodruff 1919. NEW STATE RECORD. Counties: Alamance, Beaufort, Bladen, Buncombe, Cabarrus, Edgecombe, Franklin, Harnett, Mecklenburg, Nash, Northampton, Pitt, Polk, Randolph, Wake, Warren, Watauga. Seasonal distribution: 23 April–16 July, [11 Sept. at UV-light (NCSU)]. Host associations: *Fagus grandifolia, Quercus falcata, Q. laurifolia, Q. nigra**, *Q. palustris, Q. phellos**.

Ophiderma evelyna Woodruff 1919. Fig. 9. Counties: Alamance, Bladen, Cabarrus, Greene, Harnett, Johnston, Lenoir, Mecklenburg, Montgomery, Nash, Pitt, Ran-

dolph, Wake, Washington, Wayne, Wilson. Seasonal distribution: late March–23–30 June. Host associations: *Quercus alba, Q. falcata*, Q. marilandica*, Q. nigra, Q. palustris, Q. phellos**.

Ophiderma flava Goding 1893. Counties: Ashe, Buncombe-Haywood [as "Mt. Pisgah," which is on the border of these counties], Macon, Watauga. Seasonal distribution: 1 June–31 August. Host associations: *Quercus alba*, Q. rubra.*

Ophiderma flavicephala Goding 1893. Counties: Alamance, Beaufort, Buncombe, Cabarrus, Durham, Franklin, Hoke, Lenoir, Nash, Pitt, Rutherford, Wake, Wayne, Wilkes, Wilson, Yadkin. Seasonal distribution: 23 April–18 June. Host associations: *Quercus alba, Q. coccinea, Q. falcata*, Q. nigra*, Q. palustris, Q. phellos*, Q. rubra* var. *ambigua* (as *borealis*), *Q. stellata.*

Ophiderma grisea Woodruff 1919. Counties: Buncombe, Yancey [as "Valley of Black Mountains," which is on the Buncombe–Yancey border (USNM)]. Seasonal distribution: 18 June–9 August. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1973c) reported four species of *Quercus* as hosts.

Ophiderma pubescens (Emmons 1854) [in part as *Ophiderma flaviguttula* Goding 1893, and as *Ophiderma pubescens* var. *australis* Woodruff 1919, in Brimley 1938]. Counties: Ashe, Hoke, Jackson, Johnston, Moore, Scotland, Wake. Seasonal distribution: 24 April–26 July. Host associations: *Quercus falcata*, Q. marilandica, Q. stellata.* Notes: Brimley's (1938) record of *O. flaviguttata* [misidentification] from Raleigh [Wake County], May, was based on a specimen of *Cyrtolobus flavolatus* (NCDA).

Ophiderma salamandra Fairmaire 1846. Counties: Ashe, Burke, Greene, Harnett, Johnston, Lee, Nash, Pasquotank, Wake, Warren, Watauga, Wayne, Wilson. Seasonal distribution: 18 April–31 August. Host associations: *Quercus falcata, Q. nigra, Q. palustris, Q. phellos*, Q. rubra, Q. stellata, Q. velutina*.*

Platycotis vittata (Fabricius 1803) [as *Platycotis vittata* var. *quadrivittata* (Say 1830) in Brimley 1938]. Fig. 7. Counties: Alamance, Alexander, Alleghany, Anson, Ashe, Avery, Bladen, Buncombe, Burke, Cabarrus, Caswell, Catawba, Chatham, Cherokee, Chowan, Clay, Columbus, Craven, Cumberland, Dare, Durham, Forsyth, Franklin, Gaston, Graham, Granville, Guilford, Halifax, Haywood, Henderson, Hertford, Hoke, Iredell, Jackson, Lee, Lenoir, Lincoln, Macon, Martin, Mecklenburg, Montgomery, Moore, Nash, New Hanover, Northampton, Onslow, Pasquotank, Pitt, Randolph, Robeson, Rockingham, Sampson, Stanly, Stokes, Surry, Swain, Vance, Wake, Warren, Watauga, Wilkes, Wilson, Yadkin, Yancey. Seasonal distribution: 16 January–29 December. Host associations: *Betula* sp.*, *Castanea dentata*, Fagus* sp.*, *Quercus alba*, Q. falcata*, Q. incana*, Q. laevis, Q. margarettiae, Q. nigra*, Q. palustris*, Q. phellos, Q. rubra*, Q. rubra* var. *ambigua, Q. stellata*, Q. velutina, Q. virginiana**.

Publilia concava (Say 1824). Fig. 10 (right). Counties: Ashe, Avery, Buncombe, Burke, Cherokee, Graham, Haywood, Henderson, Jackson, Macon, Madison, McDowell, Mitchell, Swain, Watauga, Wilkes, Yadkin. Seasonal distribution: late May–7 October. Host associations: *Ambrosia artemisiifolia*, A.* sp.*, *Eupatorium* sp.*, *Helianthus* sp.*, *Solidago* sp.* Notes: Brimley's (1938) specimen from "Spruce" is actually labelled "Sunburst" (Haywood County: NCDA).

Publilia reticulata Van Duzee 1908. Counties: Ashe, Avery, Buncombe, Caldwell, Haywood, Henderson, Jackson, Transylvania, Wake, Watauga, Yancey (as "Black Mountains," which is on the Buncombe–Yancey border (USNM)]. Seasonal distribution: 29 April–4 October. host associations: no data for North

Carolina. Notes: Hosts reported elsewhere include members of the Asteracae (Kopp and Yonke 1973b).

Smilia camelus (Fabricius 1803). Counties: Burke, Greene, Hoke, Mecklenburg, Moore, Pender, Robeson, Sampson, Wake, Watauga. Seasonal distribution: 24 April–25 September. Host associations: *Quercus falcata**, *Q. laevis**, *Q. nigra**, *Q. stellata.* Notes: Brimley's (1938) record of this species from Linville Falls [Caldwell County] was not verified by the present authors.

Smilia fasciata Amyot and Serville 1843. NEW STATE RECORD. Counties: Alamance, Beaufort, Cabarrus, Chatham, Craven, Davidson, Franklin, Gaston, Harnett, Johnston, Lenoir, Mecklenburg, Moore, Nash, Orange, Pasquotank, Pender, Rockingham, Wake, Warren, Wayne, Wilson. Seasonal distribution: 2 April–5 September. Host associations: *Carya illinoinensis, Quercus coccinea, Q. falcata**, *Q. nigra**, *Q. palustris**, *Q. phellos**, *Q. stellata**, *Q. velutina.*

[*Spissistilus femoratus* (Fairmaire 1846)]. Records of this species [as *Ceresa angulata* (Walker 1851)] in North Carolina (Van Duzee 1917, Brimley 1938) were not verified by the present authors.

Spissistilus festinus (Say 1830) [as *Stictocephala festina* (Say) in Brimley 1938]. Counties: Alexander, Anson, Beaufort, Bertie, Bladen, Brunswick, Buncombe, Cabarrus, Caldwell, Camden, Carteret, Catawba, Chatham, Chowan, Cleveland, Columbus, Craven, Cumberland, Currituck, Dare, Davie, Duplin, Durham, Edgecombe, Franklin, Gaston, Gates, Granville, Greene, Halifax, Harnett, Haywood, Henderson, Hoke, Iredell, Jackson, Johnston, Jones, Lee, Lincoln, Madison, Martin, Mecklenburg, Mitchell, Montgomery, Moore, Nash, New Hanover, Onslow, Orange, Pamlico, Pasquotank, Pender, Perquimans, Polk, Randolph, Robeson, Rockingham, Rowan, Sampson, Scotland, Stanly, Swain, Transylvania, Tyrrell, Union, Vance, Wake, Warren, Washington, Wayne, Wilkes, Wilson. Seasonal distribution: 19 February–19 December. Host associations: *Arachis hypogaea**, *Aster ericoides, Glycine max**, *Helianthus* sp., *Lespedeza* sp.*, *Medicago sativa**, *Phaseolus vulgaris**, *Sarracenia flava, Solidago* sp. Notes: This species is commonly known as the "three-cornered alfalfa hopper." Hargrove's (1986) record of *S. festinus* from Coweeta, Macon County (on *Robinia pseudoacacia*), was not verified by the present authors.

[*Spissistilus rotundata* Stål 1869]. Brimley's (1938) records of *Stictocephala rotundata* Stål in North Carolina (Raleigh [Wake County] and Southern Pines [Moore County]) were not verified by the present authors.

[*Spissistilus uniformis* (Fairmaire 1846), misidentification]. Brimley's (1938) records of *Ceresa uniformis* Fairmaire actually refer to *Hadrophallus borealis*; these include one female in NCDA from Balsam [Jackson County], 14–18 September.

Stictocephala bisonia Kopp and Yonke 1977 [as *Ceresa bubalus* (Fabricius 1794), misidentification, in Brimley 1938; as *Stictocephala bubalus* (Fabricius), misidentification, in Kopp and Yonke 1973b; *Stictocephala bisonia* Kopp and Yonke 1977 (Kopp and Yonke 1977); as *S. alta* (Walker 1851) in Andrade 1997 (questionable synonymy, see "Notes," below)]. Counties: Alleghany, Ashe, Avery, Beaufort, Buncombe, Haywood, Madison, Mitchell, Montgomery, Stanly, Surry, Wake, Warren, Watauga. Seasonal distribution: 16 July–30 September. Host associations: *Glycine max.* Notes: This species is commonly known as the "buffalo treehopper." Recently, Andrade (1997) considered *S. bisonia* to be a junior synonym of *S. alta* (Walker 1851). We believe this synonymy is insufficiently justified in light of the need to examine the male genitalia to reliably identify many species of the tribe Cere-

sini. The holotype of *Ceresa alta* Walker is of ambiguous identity, being a female specimen from an unspecified locality. On the other hand, the identity of the male holotype of *S. bisonia* Kopp and Yonke is definitive, and this type is accompanied by 45 paratypes (males and females), all from Columbia, Missouri, USA.

[*Stictocephala brevicornis* (Fitch 1856)]. Records of this species in North Carolina were not verified by the present authors. Brimley's (1938) record of *Ceresa brevicornis* Fitch (Swannanoa, Buncombe County, May) probably referred to *Stictocephala brevitylus* (Van Duzee); Kopp and Yonke's (1973b: map) record may be based on Brimley's publication. Hargrove (1986) also listed this treehopper from Coweeta, Macon County, on *Robinia pseudoacacia.*

[*Stictocephala brevis* (Walker 1851)]. Notes: Brimley's (1938) record of this species in North Carolina (as *Ceresa brevis* Walker) has not been verified by the present authors. One specimen (Swannanoa, Buncombe County, 21 May: NCDA) identified as *Ceresa brevis* Walker by Brimley is actually *Stictocephala brevitylus,* however, Brimley's published record gave no locality or date.

Stictocephala brevitylus (Van Duzee 1908) [as *Ceresa brevitylus* Van Duzee in Brimley 1938]. Counties: Alleghany, Anson, Avery, Brunswick, Buncombe, Cabarrus, Caswell, Catawba, Chatham, Cumberland, Currituck, Dare, Durham, Forsyth, Granville, Harnett, Haywood, Henderson, Hertford, Jackson, McDowell, Mecklenburg, Moore, New Hanover, Pasquotank, Randolph, Stanly, Swain, Wake, Washington, Watauga, Wilkes, Yadkin, Yancey. Seasonal distribution: 5 April–2 July. Host associations: *Aster* sp., *Ceanothus* sp., *Chrysanthemum leucanthemum, Helianthus* sp.*, *Morus* sp., *Quercus falcata, Robinia pseudoacacia, Rubus argutus**, *Sarracenia flava, Smilax* sp.*, *Solanum tuberosum, Vaccinium* sp. (as *Polycodium* sp.), *Vitis* sp. 'French hybrid'.

Stictocephala diceros (Say 1824) [as *Ceresa diceros* (Say) in Brimley 1938]. Counties: Ashe, Buncombe, Cabarrus, Caldwell, Durham, Granville, Haywood, Iredell, McDowell, Mecklenburg, Wake, Watauga. Seasonal distribution: 8 June–6 October. Host associations: *Sambucus canadensis.*

[*Stictocephala diminuta* Van Duzee 1908]. North Carolina records of this species were not verified by the present authors. Brimley's (1938) record of *S. diminuta* in Raleigh [Wake County], July, probably represents *S. brevitylus.*

Stictocephala lutea (Walker 1851). Counties: Alleghany, Avery, Bladen, Brunswick, Buncombe, Burke, Carteret, Caswell, Chatham, Cumberland, Duplin, Haywood, Hoke, Jackson, Johnston, Madison, Mecklenburg, Moore, New Hanover, Onslow, Pender, Sampson, Scotland, Stanly, Transylvania, Vance, Wake, Washington, Watauga. Seasonal distribution: 24 February–16 September. Host associations: *Quercus falcata* (suckers).

Stictocephala militaris (Gibson and Wells 1917). NEW STATE RECORD. Fig. 6. Counties: Bladen, Craven, Hyde, Johnston, Mecklenburg, Pitt, Wake. Seasonal distribution: 19 June–16 October. Host associations: *Cercis canadensis, Prunus serotina.*

Stictocephala palmeri (Van Duzee 1908) [as *Ceresa palmeri* Van Duzee in Brimley 1938]. Counties: Avery-Caldwell-Watauga [as "Grandfather Mountain," which is on the border of these three counties (NCSU)], Buncombe, Graham, Macon, McDowell-Yancey [as "Buck Creek Gap," which is on the border of these counties (NCSU)], Stanly, Wake. Seasonal distribution: 21 July–29 September. Host associations: no data for North Carolina. Notes: Elsewhere, *Carya* is the oviposition host (Funkhouser

1917)—feeding occurs also on other woody hosts (Kopp and Yonke 1973b).

Stictocephala stimulea (Van Duzee 1914). NEW STATE RECORD. Counties: Cabarrus, Pender, Wake. Seasonal distribution: 1–31 May. Host associations: *Vitis* prob. *vulpina* [ovipositing in canes].

[*Stictocephala substriata* (Walker 1851)]. Brimley's (1938) records of this species in North Carolina (Raleigh [Wake County] and Southern Pines [Moore County]) were not verified by the present authors.

Stictocephala taurina (Fitch 1856) [as *Ceresa taurina* (Fitch) in Brimley 1938]. Counties: Ashe, Avery, Buncombe, Forsyth, Madison, Mitchell, Surry, Wake, Watauga. Seasonal distribution: 19–20 June–18 September. Host associations: *Helianthus* sp., *Rubus* sp., *Sambucus canadensis, Smilax* sp.*

Stictocephala tauriniformis Caldwell 1949. NEW STATE RECORD. Counties: Haywood. Seasonal distribution: 14 September. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1973b) reported *Quercus* and *Tilia* as hosts.

Stictolobus minutus (Funkhouser 1915) [as *Stictolobus subulatus* (Say 1830) in Brimley 1938 and Kopp and Yonke 1973b]. Counties: Pender, Wake. Seasonal distribution: early July. Host associations: no data for North Carolina. Notes: Elsewhere, Kopp and Yonke (1973b) reported *Taxodium distichum* (L.) L. Richard as a host.

Telamona ampelopsidis (Harris 1841). Counties: unknown, as "NC" on data label (USNM). Seasonal distribution: unknown. Host associations: no data for North Carolina. Notes: Early reports of this species in North Carolina (Ball 1931; Brimley 1938) apparently refer to *T. maculata* Van Duzee, based on a specimen misidentified by C. S. Brimley as *T. ampelopsidis* (NCDA). Kopp and Yonke (1974: map), who also reported the species in North Carolina, listed its host as *Parthenocissus quinquefolia* (L.) Planchon.

Telamona collina (Walker 1851). NEW STATE RECORD. Counties: Wake. Seasonal distribution: 18–22 May. Host associations: *Platanus occidentalis.*

[*Telamona concava* Fitch 1851, misidentification]. Records of *Telamona concava* from Linville Falls (Caldwell County, June 1920: NCDA) (Brimley 1942, Wray 1967), actually refer to *Heliria gibberata.*

Telamona decorata Ball 1903. NEW STATE RECORD. Counties: Ashe, Henderson, Watauga. Seasonal distribution: 19–20 June–13 September. Host associations: *Castanea dentata, Quercus alba, Q. rubra.*

Telamona dubiosa Van Duzee 1916. NEW STATE RECORD. Counties: Bladen. Seasonal distribution: 21 September–11 October. Host associations: no data for North Carolina. Funkhouser (1917) listed *Quercus alba* as a host.

Telamona extrema Ball 1903. NEW STATE RECORD. Counties: Carteret, Wake, Yadkin. Seasonal distribution: 13–29 May. Host associations: no data for North Carolina. Notes: Hosts reported elsewhere include two species of *Quercus* (Kopp and Yonke 1974).

Telamona maculata Van Duzee 1908. NEW STATE RECORD. Counties: Ashe, Wake. Seasonal distribution: 10 May–18 July. Host associations: no data for North Carolina. Notes: Hosts elsewhere include three species of *Quercus* (Kopp and Yonke 1974).

Telamona monticola (Fabricius 1803). Counties: Ashe, Avery, Buncombe, Burke, Caldwell, Columbus, Hoke, Johnston, Macon, Robeson, Surry, Vance, Wake, Watauga. Seasonal distribution: 20 April–18 October. Host associations: *Quercus falcata, Q. margarettiae, Q. nigra**, *Q. rubra**, *Q. stellata, Vitis rotundifolia.*

Telamona reclivata Fitch 1851. Counties: Ashe, Buncombe, Macon, Mecklenburg,

Wake. Seasonal distribution: 2 June–31 August. Host associations: *Quercus alba.*

[*Telamona salvini* Distant 1879]. Records (Ball 1931, Brimley 1938) of *T. salvini* in North Carolina (Black Mountains) were not verified by the present authors, but the species is known to occur in Charleston County, South Carolina (NCSU, 1 specimen).

[*Telamona tiliae* Ball 1925]. Records of *T. tiliae* in "North Carolina" (Ball 1931, Brimley 1938) seem to be based, at least in part, on a specimen (Blowing Rock [Watauga County], 13 Sept., NCDA) identified by C. S. Brimley as *T. tiliae* which is actually *T. decorata.* Presence of this species in North Carolina remains unconfirmed.

Telamona unicolor Fitch 1851. Counties: Bertie, Bladen, Buncombe–Yancey [as "Black Mountains" which is on the Buncombe–Yancey border], Columbus, Hoke, Macon, Mecklenburg, Wake. Seasonal distribution: 29 April–27 October. Host associations: *Carya illinoinensis**, *C.* sp.*.

Telamona westcotti Goding 1893. Counties: Henderson, Union. Seasonal distribution: 25–30 June–5 September. Host associations: no data for North Carolina. Notes: Hosts reported elsewhere include *Quercus, Tilia,* and *Ulmus* (Kopp and Yonke 1974).

Thelia bimaculata (Fabricius 1794). Counties: Alexander, Ashe, Avery, Buncombe, Graham, Haywood, Jackson, Lincoln, Macon, McDowell, Mecklenburg, Swain, Wake, Watauga. Seasonal distribution: 10 June–19 October. Host associations: *Robinia pseudoacacia**.

Tortistilus abnormus (Caldwell 1949). NEW STATE RECORD. Counties: Durham, Stanly. Seasonal distribution: 13–21 July. Host associations: no data for North Carolina.

[*Tortistilus inermis* (Fabricius 1775)]. Brimley's (1938) record of *T. inermis* (as *Stictocephala inermis*) in North Carolina was not verified by the present authors, but the species has also been recorded from two adjoining states, Virginia and Tennessee (Kopp and Yonke 1973b).

Tortistilus lateralis (Funkhouser 1936). NEW STATE RECORD. Counties: Bladen. Seasonal distribution: 8–22 September. Host associations: no data for North Carolina.

Tylopelta gibbera (Stål 1869) [as *Tylopelta brevis* Van Duzee 1908, in Brimley 1938; as *Tylopelta americana* (Goding 1893) in Kopp and Yonke 1973a]. Counties: Buncombe, Haywood, New Hanover, Swain, Wake. Seasonal distribution: 16 April–27 September. Host associations: *Desmodium* sp.

Vanduzea arquata (Say 1830) [as *V. arcuata* (sic) in Brimley 1938]. Fig. 8. Counties: Alamance, Alexander, Alleghany, Ashe, Avery, Bladen, Buncombe, Caldwell, Caswell, Catawba, Chatham, Cherokee, Clay, Durham, Forsyth, Graham, Haywood, Jackson, Lincoln, Macon, Madison, Mecklenburg, Mitchell, Orange, Polk, Richmond, Rockingham, Sampson, Surry, Swain, Union, Wake, Watauga, Wilkes, Yancey. Seasonal distribution: [? late March (NCSU)], 9 May–27 October. Host associations: *Robinia pseudoacacia**.

Vanduzea triguttata (Burmeister 1836). Counties: Hoke, Johnston, Lee, Moore, New Hanover, Pender, Stanly, Wake. Seasonal distribution: 17 June–27 September. Host associations: *Lespedeza* sp.*

Xantholobus intermedius (Emmons 1854). Counties: Ashe, Buncombe–Yancey [as "Valley of Black Mountains," which is on the Buncombe–Yancey border (USNM)], Wake. Seasonal distribution: 4 May–7 July. Host associations: *Betula alleghaniensis* (as *B. lutea*), *Quercus phellos**.

Xantholobus lateralis (Van Duzee 1908) [as *Cyrtolobus lateralis* Van Duzee in Brimley 1938]. Counties: Ashe, Burke, Caldwell, Lee, Mecklenburg, Watauga. Seasonal distribution: 3 May–6 July. Host associations: *Betula* sp., *Quercus alba.*

Xantholobus muticus (Fabricius 1777) [as

Cyrtolobus muticus (Fabricius) in Brimley 1938]. Counties: Camden, Chatham, Duplin, Forsyth, Franklin, Gates, Greene, Hertford, Lee, Moore, Nash, Northampton, Randolph, Rutherford, Wake, Warren, Wayne, Wilson. Seasonal distribution: 18 April–14 July. Host associations: *Quercus alba**, *Q. laevis, Q. prinus, Q. stellata**.

Xantholobus nitidus (Van Duzee 1908). Counties: Bladen, Forsyth, Johnston, Moore, Sampson, Wake, Wilkes. Seasonal distribution: 17 May–19 June. Host associations: no data for North Carolina.

Host Plant Index for North Carolina Treehoppers

Plant scientific name, common name(s) (Family): associated treehopper species.

Ambrosia artemisiifolia L., ragweed (Asteraceae): *Acutalis tartarea, Entylia carinata**, *Publilia concava**.

Ambrosia sp., ragweed (Asteraceae): *Entylia carinata, Publilia concava**.

Arachis hypogaea L., peanut, common peanut, goober, groundnut, grass nut, earth nut, monkey nut, pindar (Fabaceae): *Spissistilus festinus**.

Arundinaria sp., bamboo, cane (Poaceae): *Acutalis tartarea.*

Aster ericoides L., heath aster (Asteraceae): *Spissistilus festinus.*

Aster sp., aster, Michaelmas daisy, starwort, frost flower (Asteraceae): *Entylia carinata, Stictocephala brevitylus.*

Betula alleghaniensis Britton, yellow birch, gray birch (Betulaceae): *Xantholobus intermedius.*

Betula sp., birch (Betulaceae): *Carynota marmorata, Platycotis vittata**, *Xantholobus lateralis.*

Bidens bipinnata L., Spanish needles (Asteraceae): *Entylia carinata.*

Bidens coronata (L.) Britton, beggar ticks, beggar's ticks (Asteraceae): *Acutalis tartarea, Entylia carinata.*

Bidens sp., beggar ticks, beggar's ticks, bur marigold, water marigold, pitchforks, Spanish needles, stick-tights, tickseed (Asteraceae): *Entylia carinata.*

Carya illinoinensis (Wangenh.) K. Koch, pecan (Juglandaceae): *Carynota mera, Microcentrus caryae**, *M. perditus, Smilia fasciata, Telamona unicolor**.

Carya sp., hickory (Juglandaceae): *Carynota mera**, *Enchenopa binotata* complex, *Microcentrus caryae, Telamona unicolor**.

Castanea dentata (Marshall) Borkh., American chestnut (Fagaceae): *Atymna castaneae**, *Platycotis vittata**, *Telamona decorata.*

Castanea pumila (L.) P. Miller, chinquapin (Fagaceae): *Atymna castaneae**.

Ceanothus sp., redroot (Rhamnaceae): *Stictocephala brevitylus.*

Cercis canadensis L., eastern redbud, redbud, Judas tree (Fabaceae): *Enchenopa binotata* complex*, *Stictocephala militaris.*

Chrysanthemum leucanthemum L., ox-eye daisy, white daisy, marguerite, whiteweed (Asteraceae): *Stictocephala brevitylus.*

Conyza canadensis (L.) Cronquist, horseweed, hogweed, butterweed (Asteraceae): *Entylia carinata, Micrutalis calva.*

Dahlia sp., dahlia (Asteraceae): *Entylia carinata.*

Desmodium sp., beggar lice, beggar ticks, beggar's ticks, tick trefoil, tick clover (Fabaceae): *Tylopelta gibbera.*

Erechtites hieraciifolia (L.) Raf. ex DC., fireweed (Ranuculaceae): *Entylia carinata**.

Erigeron annuus (L.) Persoon, daisy fleabane, sweet scabious, white-top, fleabane (Asteraceae): *Micrutalis calva.*

Erigeron sp., fleabane (Asteraceae): *Entylia carinata.*

Eupatorium capillifolium (Lam.) Small, dog-fennel (Asteraceae): *Acutalis tartarea, Entylia carinata.*

Eupatorium pilosum Walter, thoroughwort, boneset (Asteraceae): *Entylia carinata.*

Eupatorium sp., thoroughwort, boneset

(Asteraceae): *Entylia carinata, Publilia concava**.

Fagus grandifolia J. F. Ehrhart, beech, American beech (Fagaceae): *Ophiderma definita.*

Fagus sp., beech (Fagaceae): *Microcentrus caryae, Platycotis vittata.*

Gleditsia triacanthos L., honey locust, sweet locust, honeyshuck (Fabaceae): *Micrutalis calva**.

Glycine max (L.) Merrill, soybean, soja bean, soya bean (Fabaceae): *Entylia carinata, Micrutalis calva, Spissistilus festinus**, *Stictocephala alta.*

Helianthus annuus L., sunflower, common sunflower, mirasol (Asteraceae): *Entylia carinata.*

Helianthus sp., sunflower (Asteraceae): *Acutalis tartarea, Entylia carinata, Publilia concava, Spissistilus festinus, Stictocephala brevitylus**, *S. taurina.*

Helianthus tuberosus L., Jerusalem artichoke, girasole (Asteraceae): *Entylia carinata**.

Juglans nigra L., black walnut (Juglandaceae): *Enchenopa binotata* complex*.

Lespedeza sp., bush clover (Fabaceae): *Spissistilus festinus**, *Vanduzea triguttata**.

Liriodendron tulipifera L., tulip tree, tulip poplar, whitewood, yellow poplar (Magnoliaceae): *Enchenopa binotata* complex.

Medicago sativa L., alfalfa, lucerne (Fabaceae): *Campylenchia latipes, Spissistilus festinus**.

Morus sp., mulberry (Moraceae): *Stictocephala brevitylus.*

Phaseolus vulgaris L., common bean, kidney bean, green bean, snap bean, haricot, French bean, frijol, runner bean, string bean, salad bean, wax bean (Fabaceae): *Spissistilus festinus**.

Physalis sp., ground cherry (Solanaceae): *Micrutalis malleifera.*

Platanus occidentalis L., eastern sycamore, sycamore, button wood, buttonball, American plane-(Platanaceae): *Telamona collina.*

Prunus serotina J. F. Ehrhart, black cherry, wild black cherry, rum cherry, (Rosaceae): *Stictocephala militaris.*

Quercus alba L., white oak (Fagaceae): *Archasia auriculata**, *A. belfragei**, *Atymna querci**, *Cyrtolobus auroreus**, *C. dixianus, C. fuscipennis**, *Cyrtolobus griseus, C. maculifrontis**, *C. pallidifrontis, C. tuberosus**, *C. vau**, *Glossonotus univittatus, Ophiderma evelyna, O. flava**, *O. flavicephala, Platycotis vittata**, *Telamona decorata, T. reclivata, Xantholobus lateralis, X. muticus**.

Quercus coccinea Muenchh., scarlet oak (Fagaceae): *Cyrtolobus fuliginosus, Ophiderma flavicephala, Smilia fasciata.*

Quercus falcata Michaux, southern red oak, Spanish oak, Spanish red oak (Fagaceae): *Stictocephala lutea, Telamona monticola, Cyrtolobus arcuatus**, *C. dixianus, C. fenestratus**, *C. fuliginosus**, *C. inermis**, *C. maculifrontis, Glossonotus acuminatus**, *Ophiderma definita, O. evelyna**, *O. flavicephala**, *O. pubescens**, *O. salamandra, Platycotis vittata**, *Smilia camelus**, *S. fasciata**, *Stictocephala brevitylus, S. lutea, Telamona monticola.*

Quercus incana Bartram, bluejack oak, upland willow oak, bluejack, turkey oak, high-ground willow oak, sand jack (Fagaceae): *Platycotis vittata**.

Quercus laevis Walter, turkey oak, Catesby oak (Fagaceae): *Cyrtolobus fenestratus, C. ovatus**, *Platycotis vittata, Smilia camelus**, *Xantholobus muticus.*

Quercus laurifolia Michaux, laurel oak, Darlington oak, laurel-leaved oak (Fagaceae): *Ophiderma definita.*

Quercus margarettiae Ashe ex Small, scrubby post oak (Fagaceae): *Cyrtolobus fenestratus, C. tuberosus, Telamona monticola, Platycotis vittata.*

Quercus marilandica Muenchh., blackjack oak, blackjack, jack oak (Fagaceae): *Cyrtolobus fenestratus**, *C. inermis, C. ovatus**, *C. tuberosus, Ophiderma evelyna**, *O. pubescens.*

Quercus nigra L., water oak, possum oak (Fagaceae): *Archasia auriculata, Cyrtolobus fenestratus**, *C. fuscipennis, C. toga-*

*tus**, *C. tuberosus, Ophiderma definita**, *O. evelyna, O. flavicephala**, *O. salamandra, Platycotis vittata**, *Smilia camelus**, *S. fasciata**, *Telamona monticola**.

Quercus palustris Muenchh., pin oak, Spanish oak (Fagaceae): *Cyrtolobus clarus**, *C. dixianus, C. fenestratus, C. fuliginosus, C. funkhouseri, Entylia carinata, Ophiderma definita, O. evelyna, O. flavicephala, O. salamandra, Platycotis vittata, Smilia fasciata**.

Quercus phellos L., willow oak (Fagaceae): *Archasia belfragei, Cyrtolobus arcuatus, C. clarus**, *C. fenestratus**, *C. fuliginosus, C. togatus**, *Ophiderma definita**, *O. evelyna**, *O. flavicephala**, *O. salamandra**, *Platycotis vittata, Smilia camelus, S. fasciata**, *Xantholobus intermedius**.

Quercus prinus L., chestnut oak, rock chestnut oak, basket oak (Fagaceae): *Cyrtolobus auroreus, C. tuberosus, C. vau, Xantholobus muticus.*

Quercus rubra L. (see also var. *ambigua*, gray oak or northern red oak, below), red oak (Fagaceae): *Cyrtolobus fenestratus**, *C. pulchellus, C. togatus, Glossonotus univittatus, Ophiderma flava, O. salamandra, Platycotis vittata**, *Telamona decorata, T. monticola.*

Quercus rubra var. *ambigua* (Gray) Fern., gray oak, northern red oak (Fagaceae): *Ophiderma flavicephala, Platycotis vittata.*

Quercus stellata Wangenh., post oak (Fagaceae): *Atymna querci**, *Cyrtolobus dixianus**, *C. fuliginosus, C. griseus, C. inermis, C. pallidifrontis**, *C. togatus, C. tuberosus, C. vau, Ophiderma flavicephala, O. pubescens, O. salamandra, Platycotis vittata**, *Smilia camelus, S. fasciata**, *Telamona monticola, Xantholobus muticus**.

Quercus velutina Lam., black oak, yellow-bark oak, quercitron (Fagaceae): *Archasia auriculata**, *Cyrtolobus fenestratus, C. fuliginosus, Ophiderma salamandra**, *Platycotis vittata, Smilia fasciata.*

Quercus virginiana P. Miller, live oak, southern live oak (Fagaceae): *Cyrtolobus fenestratus, C. tuberosus, Platycotis vittata**.

Robinia pseudoacacia L., black locust, false acacia, yellow locust (Fabaceae): *Enchenopa binotata* complex*, *Micrutalis calva, Stictocephala brevitylus, Thelia bimaculata**, *Vanduzea arquata**.

Rubus argutus Link, blackberry (Rosaceae): *Stictocephala brevitylus**.

Rubus sp., bramble (Rosaceae): *Stictocephala taurina.*

Salix nigra Marshall, black willow (Salicaceae): *Micrutalis calva.*

Sambucus canadensis L., elderberry, American elderberry, sweet elderberry, (Caprifoliaceae): *Stictocephala diceros, S. taurina.*

Sarracenia flava L., yellow pitcher plant, trumpets, watches, biscuit-flower, trumpetleaf, umbrella-trumpets, huntsman's horn (Sarraceniaceae): *Spissistilus festinus, Stictocephala brevitylus.*

Silphium sp., rosinweed (Asteraceae): *Entylia carinata.*

Smilax sp., greenbrier, catbrier (Liliaceae): *Stictocephala brevitylus**, *S. taurina**.

Solanum tuberosum L., potato, Irish potato, white potato (Solanaceae): *Entylia carinata, Stictocephala brevitylus.*

Solidago sp., goldenrod (Asteraceae): *Acutalis tartarea, Campylenchia latipes, Entylia carinata, Micrutalis calva, Publilia concava**, *Spissistilus festinus.*

Vaccinium sp., blueberry, huckleberry, cranberry, bilberry (Ericaceae): *Stictocephala brevitylus.*

Verbesina alternifolia (L.) Britton ex Kearney, wingstem, yellow ironweed (Asteraceae): *Entylia carinata.*

Viburnum prunifolium L., black haw, sweet haw, sheepberry, nanny-berry, stagbush (Caprifoliaceae): *Enchenopa binotata* complex.

Vitis rotundifolia Michaux, muscadine grape, scuppernong grape, bullace grape (Vitaceae): *Atymna querci, Entylia carinata, Micrutalis calva, Telamona monticola.*

Vitis sp., grape (Vitaceae): *Entylia carinata.*

Vitis sp. 'French hybrid,' grape 'French hybrid' (Vitaceae): *Micrutalis calva, Stictocephala brevitylus.*

Vitis prob. *vulpina* L., frost grape, winter grape, chicken grape (Vitaceae): *Stictocephala stimulea.*

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A TURN OF THE CENTURY CONUNDRUM—REEXAMINATION OF *AEOLOTHYNNUS* ASHMEAD (HYMENOPTERA: TIPHIIDAE: THYNNINAE)

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Abstract.—The identity of the Australian thynnine genus *Aeolothynnus* Ashmead has been the source of nomenclatural confusion since the early 1900's. Its identity is reevaluated relative to other related genera, species placements are reconsidered, and one new species, ***Aeolothynnus caliventer,*** from South Australia, is described. *Asthenothynnus* is discovered to be a **new junior synonym** of *Aeolothynnus,* and Turner's concept of *Aeolothynnus* is in reality synonymous with *Thynnoturneria* Rohwer. **New combinations** of species in *Aeolothynnus* include: *Thynnus beatrix* Turner, *Asthenothynnus deductor* Turner, *Thynnus generosus* Turner, *Asthenothynnus kurandensis* Turner, *Thynnus lactarius* Turner, *Asthenothynnus lilliputianus* Turner, *Asthenothynnus maritimus* Turner, *Asthenothynnus minutissimus* Turner, *Asthenothynnus perkinsi* Turner, *Asthenothynnus pleuralis* Turner, *Thynnus pulcherrimus* Turner, and *Asthenothynnus vicarius* Turner.

Key Words: Tiphiidae, Hymenoptera, Thynninae, *Aeolothynnus, Asthenothynnus,* Australia

Many genera of Thynninae were originally based on one or a small number of species, and the original characterizations were obscure at best. One of the finest examples of the confusion resulting from these inadequate descriptions can be seen in the taxonomic literature near the turn of the century, published by taxonomists at the British Museum and at the U.S. National Museum. This confusion was largely the result of miscommunications, misinterpretations and a bit of transatlantic competition. Two generic names, *Aeolothynnus* Ashmead and *Asthenothynnus* Turner, were proposed for the same group of species. The valid generic name for these species is *Aeolothynnus* and Turner's mistaken concept of the genus *Aeolothynnus* is a very different entity later renamed *Thynnoturneria* Rohwer, which in turn has been confused with *Iswaroides* Ashmead.

Ashmead originally based *Aeolothynnus* on the new species *multiguttatus.* He described the species and genus simultaneously in one of his notorious keys (1903). As a result of his habit of describing new genera and species in very brief keys, most subsequent authors confused the identity of *Aeolothynnus.* Although Ashmead did not clearly indicate the species as new, the genus was monotypic, therefore as stated in the International Zoological Code (1985), Article 12, the generic description also applied to the species. As a result, Turner's 1908 statement that "*Ashmead gives Aeolothynnus multiguttatus Ashm., as the type of his genus but, as he has not given any description of that species, his name cannot stand.*" is incorrect. To further confuse the situation, Rohwer (1910a) subsequently recognized Ashmead's designation of *multiguttatus* and gave a new name to Turner's

concept of *Aeolothynnus* as *Turnerella*, stating that:

> *"The characters given by Ashmead in his table of the genera of Thynnidae, are sufficient to satisfy the technical requirements so this species [Aeolothynnus multiguttatus Ashmead (nec Turner)] should date from that time and be accredited to Ashmead."*
> *"Turner considering that Aelothynnus (sic!) multiguttatus Ashm, was undescribed named Thynnus cerceroides Sm. as the type of Aelothynnus. Aelothynnus multiguttatus Sm. and Thynnus cerceroides are not congeneric, which leaves Aelothynnus Turn, without a name. For this genus the name Turnerella may be used."*

Unfortunately the name *Turnerella* ran into problems of homonymy, and according to Turner (1911):

> *"My identification of Ashmead's genus, of which the type was undescribed, was incorrect, as has been pointed out by Mr. Rohwer, who renamed the genus Turnerella. That name, however, was used by Professor Cockerell for a genus of bees; his paper was published in London on the same day as Mr. Rohwer's paper was published in America, and I believe the name should be retained for the bee. I therefore have to propose a new name for the genus."*

Turner never made a new generic description for his concept of *Aeolothynnus*. The uncertainty of the situation caused Given (1959) to lament:

> *"The genus Aeolothynnus was erected by Ashmead in 1903 with the genotype A. multiguttatus. The genus was then very poorly defined and has been frequently misinterpreted by subsequent workers."*
> *"Rohwer (1910a) published the first description of the genotype, Ashmead (1903) having given mere key distinctions. Rohwer (1910a) stated that T. cerceroides and A. multiguttatus were not congeneric and therefore the genus Aeolothynnus Turner was left without a name as that name was valid for the genotype multiguttatus of Ashmead. Rohwer (1910a) proposed the name Turnerella for Turner's genus. However, this generic title was preoccupied, and both Turner (1911) and Rohwer (1910b) appreciated this at about the same time. Turner (1911) then proposed the name Eurohweria for his genus, but he was forestalled by Rohwer (1910b) who proposed the name Thynnoturneria."*

When Rohwer (1910b) renamed *Aeolothynnus*, as treated by Turner, he established Turner's concept of the group as a valid genus, particularly since none of the species placed by Turner (1910a) in *Aeolothynnus* under *cerceroides* were congeneric with *multiguttatus*. Thus the name *Thynnoturneria* Rohwer applied to the *cerceroides* group of species. Turner (1912) was not entirely pleased by this situation:

> *"I am by no means sure that the name Aeolothynnus should not be used for this genus. Ashmead in describing the genus Aeolothynnus took an undescribed species for the type. In my work on the Thynnidae I accepted Ashmead's genus, but treated the species as a nomen nudum. Mr. Rohwer, on the other hand, holds that the description of the genus covers the species also; but I cannot agree with this opinion, as Ashmead evidently did not intend the description for a specific one, and a description to be recognized should be at least intended by the author for a description of a species."*
> *"Unfortunately, A. cerceroides, Sm., selected by me as the type of the genus, does not appear to belong to the same genus as Ashmead's type. Yet if Ashmead's specific name is treated as a*

nomen nudum, A. cerceroides must be treated as the type of the genus. It is bad enough to have to recognized the very insufficient descriptions of some authors as valid, but if we are also to accept what were never intended for descriptions things would be still worse. For the present, pending some decision on the subject, I am using Rohwer's name, but do not consider that it can stand. The whole confusion is due to a want of editing in Ashmead's paper, as no editor should publish a description of a genus with an undescribed species taken for the type."

Turner's argument that Ashmead did not intend to describe *multiguttatus* as new at the same time as he described the genus was not accepted by other systematists.

Simultaneously, Turner (1910a) also named a new genus *Asthenothynnus*, based on *Thynnus pulchellus* Klug. Upon examination, *Thynnus pulchellus* turns out to be congeneric with *multiguttatus*. Therefore *Asthenothynnus* also becomes synonymous with *Aeolothynnus*. In light of this generic confusion all of the species placed variously in *Aeolothynnus, Thynnoturneria* and *Asthenothynnus* need to be reevaluated for their correct placement. Some of this replacement of species has been done below, showing new combinations as indicated. Types that have been seen and the generic placement confirmed are indicated by an asterisk (*). However, those without either indication are placed in the appropriate genus based on whether Turner himself placed them in his concept of *Aeolothynnus* or one of the subsequent generic names for that entity, or placed them in *Asthenothynnus*, which is the equivalent of Ashmead's *Aeolothynnus*.

To further clarify *Aeolothynnus* Ashmead the genus is rediagnosed and discussed below, species placements are reassigned, and a new species, *caliventer*, is described, which exhibits some very unusual thoracic modifications in the male.

Materials and Methods

Specimens were studied *in situ* or were borrowed from the following institutions: the Natural History Museum, London, S. Lewis; Hope Museum, Oxford University, C. O'Toole; and the Australian National Insect Collection, CSIRO, Canberra, ACT, I. Naumann and J. Cardale.

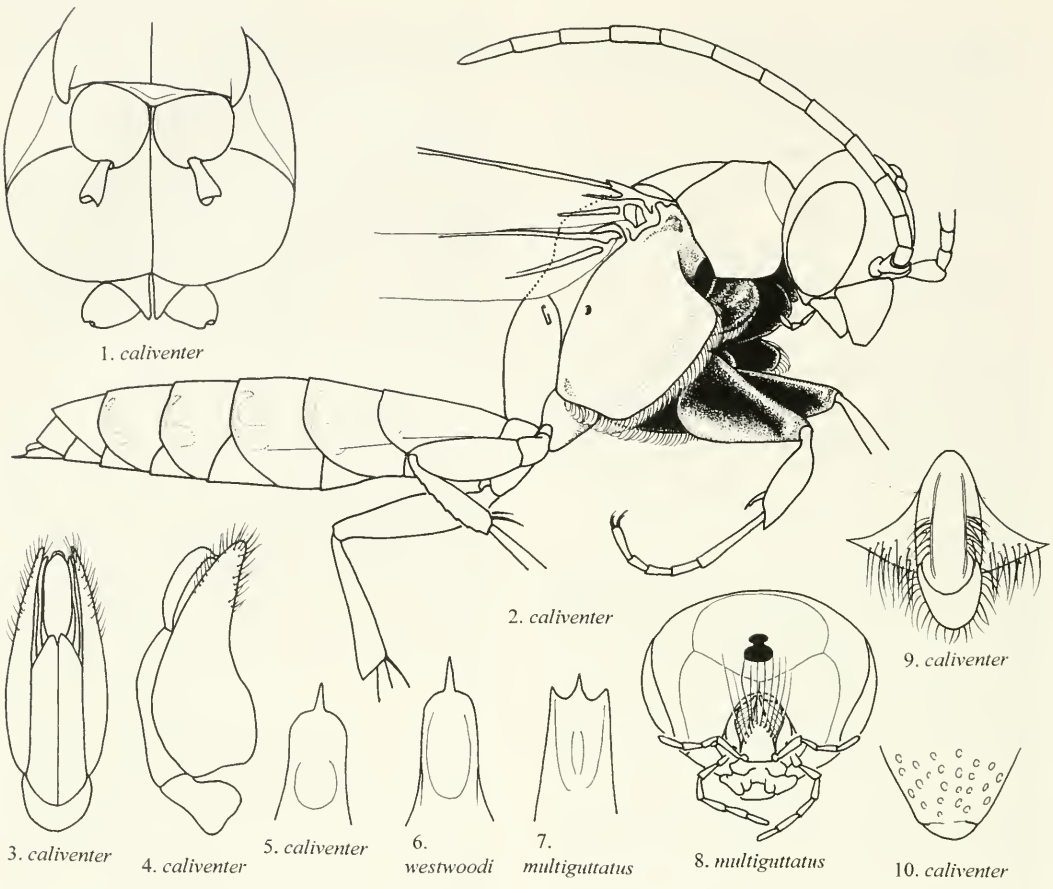
Aeolothynnus Ashmead
(Figs. 1–10)

Aeolothynnus Ashmead 1903: 101. Type species: *Aeolothynnus multiguttatus* Ashmead 1903: 101. Monobasic.

Asthenothynnus Turner 1910a: 34. Type species: *Thynnus pulchellus* Klug 1842: 20. Original designation. **New synonymy.**

Aelothynnus Rohwer 1910a. Invalid emendation of *Aeolothynnus* Ashmead 1903.

Male.—Body length 3–10 mm. *Head:* face flattened in profile, interantennal area nearly planar with clypeus; antennal sockets with dorsal antennal lobe highly reduced without carinae or transverse welt; subantennal area highly polished and impunctate; apical 7 to 9 flagellomeres somewhat arcuate or bulging along inner margin, with two small linear tyloids; clypeus nearly flat or slightly convex in profile, apical margin narrowly truncate; labrum small, medially emarginate with narrow neck-like base; tongue short unmodified, prementum with apical brush of long setae reaching back to occipital foramen; maxillary stipes with short stipal fringe originating on inner margin and extending transversely across stipes to outer margin; mandibles slender with small subapical tooth on inner margin; oral fossa extending to inner margin (Fig. 8) of mandible, widely separated from occipital carina; venter of head with large flattened and polished area, margined by carinae and surrounding the oral fossa. *Thorax:* pronotum with transverse anterior carina well-de-



Figs. 1–10. 1–5, 9–10, *Aeolothynnus caliventer*. 6, *A. westwoodi*. 7–8, *A. multiguttatus*. 1, Ventral view of male thorax. 2, Lateral view of body. 3, Ventral view of genital capsule. 4, Lateral view of genital capsule. 5–7, Apex of hypopygium. 8, Ventral view of male head. 9, Posterior view of apex of female abdomen. 10, Male apical gastral tergum.

veloped; mesepisternum and mesopleuron separated by shallow scrobal groove; propodeum without discrete dorsal surface, gently sloping posteriorly; forefemur often indented basoventrally; forecoxae globular in most species; hindcoxa with short dorsal carina. *Abdomen:* basal segment slightly convex ventrally, foreshortened, dorsally without discrete dorsal surface; apical tergum hood-like, with narrow apical lip (Fig. 10); hypopygium ventrally longitudinally grooved or trough-like, apically variable, tridentate, ligulate or unidentate (Figs. 5–7); abdominal segments smoothly tapering one to the next (Fig. 2); terga II–IV with fine sublateral transverse sulcus; spiracles not apparent; terga with W-shaped transverse sulcus or line, marked by a row of setae near posterior margin. *Genital capsule* (Figs. 3, 4): penis valves large, dilated apically and often curved; volsella large flattened and tapering apically, forming floor of capsule; digitus not apparent; parameres slender and subtriangular; gonocoxa produced into elongate, often apically notched dorsal lobe (Fig. 3); aedeagus short, originating on this lobe (Fig. 3), with short apical loop. *Color:* body black with yellow, white and red markings; vertex with oblong reddish brown spot extending diagonally from dorsal eye margin to behind hindocelli; abdomen in most species with odd

comma-shaped pale markings on most segments.

Female.—Body length 2–5 mm; *Head:* broader than long or elongate and usually appearing pinched across at eyes; clypeus narrow and linear, shorter than interantennal distance; maxillary palpus with two articles, labial palpus with three; mandible edentate and sickle-shaped. *Thorax:* pronotum subquadrate; forecoxa unmodified or narrowed and separated by deep rectangular slot (*multiguttatus*); scutum and metanotum broadly visible dorsally. *Abdomen:* tergum I and III–V with broadly W-shaped transverse sulcus; tergum II with three transverse carinae or ridges; tergum V with thin shagreened or roughened laterotergite marked by an arcuate bulge and sulcus; tergum VI with broadly or narrowly ovoid plate delimited at least laterally by carina, subtended by long tuft of setae (Fig. 9); sternum VI narrowly U-shaped. *Color:* pale brown.

Distribution.—This genus occurs throughout southern Australia in New South Wales, South Australia, Western Australia, Tasmania, Victoria, and apparently the Northern Territory, although this record needs to be confirmed.

Included species.—Thirty species are placed in *Aeolothynnus* including: *beatrix* (Turner) 1908* (*Thynnus*), **new combination**; *caliventer* Kimsey, new species; *decoratus* (Smith) 1879 (*Thynnus*); *deductor* (Turner) 1910b (*Asthenothynnus*), **new combination**; *exiguus* (Turner) 1910c (*Thynnus*); *generosus* (Turner) 1908* (*Thynnus*), **new combination**; *incensus* (Smith) 1868 (*Thynnus*); *innocuus* (Turner) 1908 (*Thynnus*); *kurandensis* (Turner) 1910d* (*Asthenothynnus*), **new combination**; *lactarius* (Turner) 1910d* (*Thynnus*), **new combination**; *leucostictus* (Turner) 1908 (*Thynnus*); *lilliputianus* (Turner) 1915a* (*Asthenothynnus*), **new combination**; *maritimus* (Turner) 1915b* (*Asthenothynnus*), **new combination**; *minutissimus* (Turner) 1910c (*Asthenothynnus*), **new combination**; *minutus* (Smith) 1859 (*Thynnus*); *multiguttatus* Ashmead 1903*; *penetratus* (Smith) 1879 (*Thynnus*); *perkinsi* (Turner) 1910d* (*Asthenothynnus*), **new combination**; *planiventris* (Turner) 1908 (*Thynnus*); *pleuralis* (Turner) 1915a (*Asthenothynnus*), **new combination**; *pulchellus* (Klug) 1842 (*Thynnus*) (=*Thynnus multipictus* Smith 1879); *pulcherrimus* (Turner) 1908* (*Thynnus*), **new combination**; *pygmaeus* (Turner) 1908 (*Thynnus*); *quadricarinatus* (de Saussure) 1867 (*Thynnus*); *rubromaculatus* (Turner) 1908 (*Thynnus*); *tenuis* (Turner) 1908 (*Thynnus*); *vicarius* (Turner) 1915a (*Asthenothynnus*), **New combination**; *westwoodi* (Guérin de Meneville) 1842 (*Agriomyia*) (=*Thynnus intricatus* Smith* 1859); *longiceps* (Smith) 1859 (*Thynnus*); *nanus* (Smith) 1879 (*Thynnus*).

Discussion.—Members of the genus *Aeolothynnus* are small-bodied and locally abundant Australian wasps. The vast majority of species average 1 cm in length or less. Thousands of individuals, both males and females, may be found on a single flowering Eucalyptus tree. Members of the genus occur in most habitats throughout at least the southern part of Australia. They are for the most part unremarkably modified. However, a new species, collected in South Australia has a bizarrely modified male. The male modifications in this species are unusual for the entire subfamily, so it is described as new below. Hosts are apparently unknown for *Aeolothynnus*. However, given the parasitic habits of the rest of the subfamily, the hosts are undoubtedly small, locally abundant, species of larval Scarabaeidae.

A number of traits are diagnostic for members of this genus. The most distinctive feature of the males is the longitudinally grooved or impressed apical abdominal sternum (hypopygium). This characteristic coupled with their smoothly tapering abdomen, and flattened face will distinguish *Aeolothynnus* males from closely related genera. *Aeolothynnus* belongs to a group of genera characterized by the presence of a transverse carina, ridge or welt, across the

apical edge of the apical abdominal tergum (epipygium), the female apical abdominal tergum is smoothly convex, narrowed, with an oval medial plate margined laterally by a carina, which is in turn subtended laterally by a long brush of setae. This group consists of *Epactiothynnus* Turner, *Tmesothynnus* Turner, *Thynnoturneria* Rohwer, *Iswaroides* Ashmead, *Gymnothynnus* Turner, *Acanthothynnus* Turner, *Doratithynnus* Turner and *Aspidothynnus* Turner. Females are problematic in this group of genera and too few are associated with males to distinguish between species level and generic characteristics.

Aeolothynnus caliventer Kimsey, new species

(Figs. 1–5, 9, 10)

Male.—Body length 8–9 mm; *Head:* face nearly flat from frons to upper clypeus; frons and vertex densely punctate, punctures small and contiguous; prementum strongly convex medially, with long medial fringe of setae; flagellum I 1.5× as long as broad; flagellum II 2.5× as long as broad; flagellum III three times as long as broad. *Thorax* (Figs. 1, 2): Pronotum extended ventrally; propleura convex; forecoxa ventrally flat and expanded sharp-edged laterally; forefemur flat, broadly expanded and rounded ventrally; mesepisternum strongly produced and flange-like, giving the thoracic venter a strongly cuplike appearance. *Abdomen:* epipygium (Fig. 10); hypopygial apex subtruncate with rounded lateral corners and short acute medial spine, ventral groove teardrop-shaped (Fig. 5). *Genital capsule* (Figs. 3, 4). *Color:* body black with pale whitish markings on apical margin of clypeus, a small spot on each antennal lobe, pronotum with small spot adjacent to tegula and on either end of transverse anterior carina; small spot at posterior angle of mesopleuron above midcoxa outlining mesopleural lamellae, and small comma-shaped lateral spot on gastral terga I–VI; vertex with small oval red spot between hindocelli and nearest eye margin; fore- and midlegs with femoral apex and tibia entirely or partly red; hindfemur medially red; hindtibia somewhat reddish medially; wing membrane untinted, veins dark brown. *Pubescence:* long erect and silvery, except dense and golden along mesepisternal edge.

Female.—Body length 5.5 mm; *Head:* head broader than long; mandible sickle-shaped and edentate. *Thorax:* pronotal disk with anterolateral corners acute, posterior margin with two submedial warts; propleura strongly convex ventrally; scutum broadly visible; scutellum flattened, length subequal to breadth; propodeum strongly convex and rounded laterally and posteriorly. *Abdomen:* tergum I with W-shaped sulcus; II with three transverse ridges; III–IV with large submedial U-shaped sulcus; pygidium narrowly longitudinally ovoid with lateral carina, with row of setae laterad of carina (Fig. 9); sternum VI apex narrowly U-shaped. *Color:* yellowish brown.

Material examined.—Holotype ♂: Australia: SA, 79 km nnw Renmark, 33°31′S 140°24′E, 9 Aug.–7 Sept. 1995, K. R. Pullen, Casuarina woodland, malaise trap. Holotype deposited in the Australian National Insect Collection (ANIC), Canberra, ACT. Paratypes: two ♂, one ♀, same data as holotype except also collected in flight intercept trap (deposited in ANIC and Bohart Museum of Entomology, University of California, Davis). These specimens derived from the Calperum Station/Bookmark Biosphere Reserve Invertebrate Survey.

Etymology.—The name refers to the peculiar modifications of the male thorax; *calix* = cup, *venter* = belly, Latin, noun.

Discussion.—The unusually modified male thorax and forefemur will serve to distinguish this species from other *Aeolothynnus* or related genera. The female is less remarkable but can be distinguished by shape of the pronotum with a small acute tooth on the anterolateral corner and posterior submedial swellings. In addition, the scutellum is relatively flat and the propleura are strongly bulging ventrally.

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NEW NORTH AMERICAN SPECIES AND RECORDS IN THE GENUS *XENOLIMOSINA* ROHÁČEK (DIPTERA: SPHAEROCERIDAE: LIMOSININAE)

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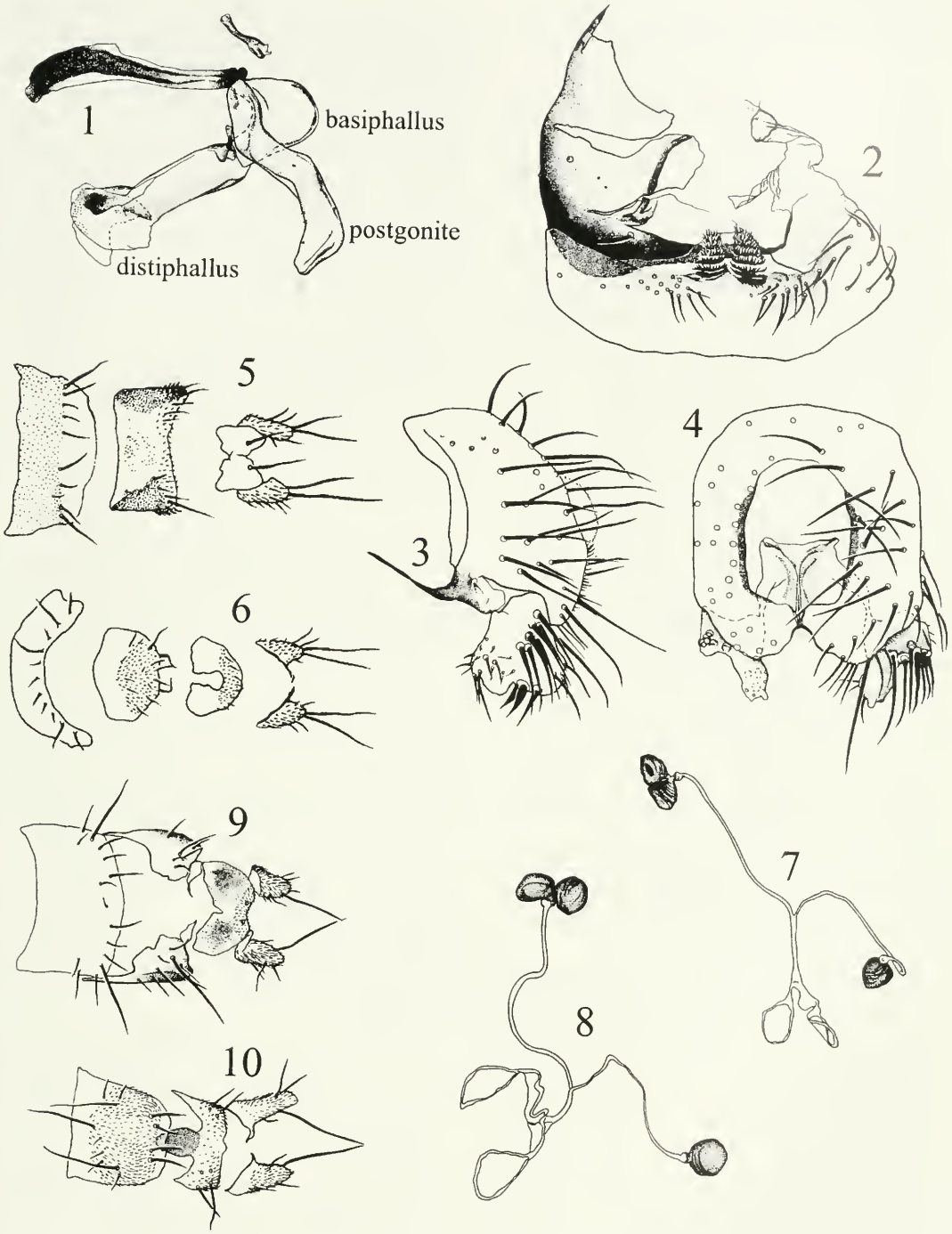
Abstract.—***Xenolimosina glabrigena,* new species,** is described from northern Florida, the female of *Xenolimosina phoba* Marshall is described, and new distributional records are given for *X. phoba* and *X. sicula Marshall.*

Key Words: Sphaeroceridae, Diptera, Florida insects

Xenolimosina Roháček is one of the most rarely collected genera of Sphaeroceridae, probably because most species seem to be active only during the colder months of the year. *Xenolimosina* previously included three species: *X. setaria* Villeneuve from Europe, *X. sicula* Marshall from Ontario, Quebec, Arkansas and California, and *X. phoba* Marshall from Quebec and Maryland. The latter species was previously known only from males, and a description of the female is given below along with new distributional records for both described North American species. A third Nearctic species, *Xenolimosina glabrigena* new species, is described from northern Florida. *Xenolimosina glabrigena* is recognisable as a *Xenolimosina* by the long exserted hind tibial bristle, small eyes, telescoping female abdomen, lack of a mid ventral bristle on the mid tibia, two spinose lobes on the male fifth sternite (Fig. 2), and the short surstylus with a long-setose posterolateral surface (Fig. 3). *Xenolimosina glabrigena* will key out to *X. sicula* in Marshall (1985), but it is distinctly different from *X. sicula* in details of the male and female genitalia. Most notably, the distiphallus of *X. glabrigena* is simple, broad and tubular, much like *X. phoba* (Marshall 1985, fig. 23), but in marked contrast to the broad, spinose and highly modified distiphallus of *X. sicula* (Marshall 1985, fig. 22) and *X. setaria* (Roháček 1983, fig. 322). Some of the characteristics of *X. glabrigena,* such as the dense pile of the male fore tibia and basitarsus, the shape of the postgonite (Fig. 1), and the sclerotization of the terminal sclerites of the female abdomen, are distinctive autapomorphies not found in the other species.

Roháček (1982) suggested that *Xenolimosina* belongs to the *Minilimosina* genus-group, and that it is probably the sister genus to *Minilimosina.* The distiphallus in *Minilimosina* species is generally simple and unadorned, suggesting that the characteristically adorned distiphallus of *X. sicula* and the European species *X. setaria* are synapomorphic, and these two species form a monophyletic group. The other two species in the genus, *X. glabrigena* and *X. phoba,* both have an elongate tubular distiphallus (Fig. 1) and a greatly enlarged costagial bristle, and together probably form the sister group to *X. setaria* plus *X. sicula.*



Figs. 1–10. 1–7, *Xenolimosina glabrigena*. 1, Aedeagus and associated structures. 2, Male sternites 5–7. 3, Male terminalia, left lateral. 4, Male terminalia, posterior. 5, Female terminalia, dorsal. 6, Female terminalia, ventral. 7, Spermathecae. 8–10. *X. phoba*. 8, Spermathecae. 9, Female terminalia, dorsal. 10, Female terminalia, ventral.

Xenolimosina glabrigena Marshall, new species
(Figs. 1–7)

Description.—Body length ca. 2.0 mm, dark brown to black with a heavy pruinosity; lower frons and gena reddish; legs brown. Interfrontal plate 1.5× as high as width at middle, bordered by 4 pairs of equal interfrontal bristles, lower two pairs weakly cruciate. Postocellar bristles absent. Eye small, height ca. 1.3× genal height, gena shining except for lower margin and a narrow vertical strip on posterior third. Palpus strongly swollen at middle, tapered at apex. Scutum with 5–6 rows of acrostichal bristles between anterior dorsocentral bristles; dorsocentral bristles in 2 pairs, anterior pair 0.6× as long as posterior pair, posterior pair equal to scutellar length. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Foreleg of male with dense yellow pile ventrally on distal half of tibia and on tarsomere one; foreleg of female unmodified. Mid tibia with long proximal anterodorsal distal anterodorsal and distal dorsal bristles. Katepisternum pruinose, with a short posterodorsal bristle and a minute anterodorsal bristle. Wing length 2.5× width; second costal sector 1.0–1.4× third; costa extending about 2 vein-widths beyond apex of R_{4+5}. Costagial bristle very long, longer than alula; alula narrow.

Male abdomen: Sternite 5 (Fig. 2) with two closely approximated posteromedial spinose patches, together making up a prominent posteromedial lobe; basal parts of spinose patches with continuous rows of spines, distal parts tapered and with smaller, separated spinules. Sternite 6 simple medially, expanded into a broad, pale part connected with a broad, thin-rimmed ring sclerite posteriorly. Epandrium (Fig. 3) uniformly setose; surstylus with a quadrate, ventrally notched anteroventral lobe, a rounded posteroventral lobe with 3 stout bristles, and a densely long-setose lateral swelling. Cercus (Fig. 4) weakly differentiated from epandrium, bare dorsally and medially, long setose ventrolaterally, cerci bent into broad posterior lobes at middle, not fused to form a subanal plate but narrowly contiguous ventrally. Subepandrial sclerite very broad, quadrate, articulating with inner ventral corners of cercus medially and posterior dorsal corners of surstyli laterally. Hypandrium with a well developed anterior apodeme; lateral arm fused with epandrium and contiguous with surstylus. Postgonite (Fig. 1) (paramere or gonostylus of authors) weakly S-shaped, distal part swollen at bend then narrowed at apex. Basiphallus simple, rounded; distiphallus simple, narrow and tubular, ending in two dark lobes and a small, weakly spinulose membrane. Ejaculatory apodeme well developed.

Female abdomen (Figs. 5–6): Tergite 8 equal in length to tergite 7, but with tripartite pigmentation, middle part small and pale. Tergite 10 pale anteromedially and posteromedially, with a bristle on each half. Cercus short, with 2 long, thin apical bristles and a long, thin dorsal bristle. Sternite 8 small, subequal in length to sternite 7 but less than half as wide, bare on anterior third, otherwise setulose and setose. Vaginal area weakly sclerotised with 2 ring-shaped sclerites. Sternite 10 densely setulose on posterior half, with a marginal row of bristles; anterior half pale and bare, with a deep, keyhole-shaped anteromedial depigmented area. Spermathecae (Fig. 7) dark, acorn-shaped; sclerotised parts of ducts very short.

Holotype.—UNITED STATES. Florida: Levy Co., Archer, on rotting fungus on sand, 17.xii.1997, S.A. Marshall (♂, University of Guelph).

Paratypes.—UNITED STATES. Florida: Marion Co., Ocala National Forest, 29.i.1986, flight intercept trap, R.&M. Marshall (2♀, University of Guelph).

Xenolimosina phoba Marshall
(Figs. 8–10)

Xenolimosina phoba Marshall 1985: 764 (male only).

Description of female terminalia (Figs. 8–10).—Tergite 8 completely divided; tergite 10 uniformly pigmented posteriorly, anteromedially pale. Cercus long, thin, with long apical, preapical and dorsal bristles. Sternite 8 large, longer than sternite 7 and over half as wide, almost entirely setulose, with 2 transverse rows of bristles. Sternite 10 with tripartite pigmentation anteriorly, middle part bare. Spermathecae (Fig. 8) acorn-shaped, sclerotised parts of ducts very short.

New records since 1985.—CANADA. Quebec, Old Chelsea, 17.x.1988, J.R. Vockeroth (1 ♀, Canadian National Collection, Ottawa). Ontario, St. Joseph's Island, Hilton Beach, fish entrail baited pan traps in hardwood forest, ix–x.1987, J. Swann (8 ♂, University of Guelph).

Comments.—The first and only female of this species was collected by Dr. Richard Vockeroth, who collected the male holotype at the same locality, and during the same month and week, twenty four years earlier.

Xenolimosina sicula Marshall

Xenolimosina sicula Marshall 1985: 765.

New distributional records.—In addition to the original records from Ontario, Quebec, California and Arkansas, specimens have been examined from the following localities: CANADA. British Columbia: Carmanah Valley. Ontario: Wellington Co., Algoma Co. UNITED STATES. New Hampshire: Strafford Co. Florida: Leon Co. All new records are from October–November.

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LIST OF SPECIES OF NEOTROPICAL MEGALOPTERA (NEUROPTERIDA)

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Abstract.—The 63 known species and subspecies of Neotropical dobsonflies and alderflies (Neuropterida: Megaloptera) are listed. Synonymy, authors, bibliographic references, and distribution of species by country and generally by province or state are included. Six localities, each of specimens thought to belong to new species, are also provided.

Resumen.—Se proporciona una lista de las 63 especies y subespecies conocidas de megalópteros (Neuropterida: Megaloptera) neotropicales. Se incluye sinonimia, autores, referencias bibliográficas y la distribución de las especies por país y generalmente también por provincia o estado. Se enumeran seis localidades de ejemplares que se cree pertenecen a especies nuevas para la ciencia.

Key Words: Corydalidae, Sialidae, dobsonflies, fishflies, alderflies, Megaloptera, Neotropics, taxonomy, species list

Megaloptera is a relatively primitive endopterygote (holometabolous) group closely related to Raphidioptera and Planipennia (Neuroptera *s. s.*). Despite being a small group, of approximately 200 (Evans 1972) to 300 species (New and Theischinger 1993) worldwide, the alpha taxonomy of the Neotropical megalopteran fauna has only recently reached a satisfactory level of knowledge. Since the most recent species list for the Neotropics (Penny 1977) does not include results of subsequent revisions, it seems useful to provide a current list of the species with references to relevant literature (i.e., original species descriptions, taxonomic revisions, significant distribution data). Species synonymy according to the most recent revision is included, as are species distributions by country and province or state if the latter were published or could be obtained. Ordering of taxa is alphabetical. Several records (*Corydalus* and *Platyneuromus*) are given as "sp. 1, sp. 2", etc., and for these locality data are given. This is in the hope that new material may be collected and the identity of these possibly new species might be established. Following Penny (1977), species of Sialidae are included in *Protosialis*. However, their exact generic position is rather uncertain at this time, as the group needs revision (e.g., Ross [1937] synonymized *Protosialis* under *Sialis*). In accordance to Cabrera and Willink's (1980) limits of the Neotropical Region, the list includes all species and subspecies recorded south of the United States–Mexico border. The corydalid species *Corydalus cornutus* (L.) and *Dysmicohermes* sp. have been collected in Texas, close to or at the Mexican border (Contreras-Ramos 1995b, 1998), so there is the possibility they occur in Mexico (Tamaulipas). Davis (1903) included Mexico as part of the distribution range of *Nigronia fasciatus*

(Walker). However, the southernmost distribution otherwise recorded for this species is in Florida (Hazard 1960).

The 63 valid species and subspecies in this list, contrast to the 46 species recorded for the Megaloptera of America north of Mexico (Evans and Neunzig 1996; 43 species [3 *Corydalus* spp. missing] in Penny et al. 1997). The highest diversity in the Neotropics lies within Corydalinae (46 spp., compared to 9 species and subspecies of Chauliodinae and 8 species of Sialidae), whereas Sialidae is the most diverse group in the Nearctic (24 spp., compared to 18 species of Chauliodinae and 4 species of Corydalinae). Four species (1 Chauliodinae and 3 Corydalinae) are shared between both regions.

Family Corydalidae

Subfamily Chauliodinae
(fishflies)

Genus *Archichauliodes* Weele 1909

1. *Archichauliodes chilensis* Kimmins.
Archichauliodes chilensis Kimmins 1954: Flint 1973; Penny 1977.

Distribution.—CHILE: Arauco, Coquimbo, Curicó, Malleco, Santiago, Valdivia, Valparaíso.

2. *Archicahuliodes pinares* Flint.
Archicahuliodes pinares Flint 1973.

Distribution.—CHILE: Concepción.

Genus *Neohermes* Banks 1908

3. *Neohermes filicornis* (Banks).
Chauliodes filicornis Banks 1903b.
Neohermes filicornis (Banks): Weele 1910; Flint 1965; Evans 1972; Contreras-Ramos 1991a, 1997.

Distribution.—UNITED STATES: Arizona, California, New Mexico; MEXICO: Baja California, Sonora.

Genus *Nothochauliodes* Flint 1983

4. *Nothochauliodes penai* Flint.
Nothochauliodes penai Flint 1983.

Distribution.—CHILE: Maule.

Genus *Protochauliodes* Weele 1909

5. *Protochauliodes bullocki* Flint.
Protochauliodes bullocki Flint 1973.

Distribution.—CHILE: Bío-Bío, Linares, Malleco, Ñuble.

6. *Protochauliodes cinerascens cinerascens* (Blanchard).
Chauliodes cinerascens Blanchard 1851.
Neohermes cinerascens (Blanchard): Banks 1908.
Protochauliodes cinerascens (Blanchard): Weele 1910; Kimmins 1954.
Protochauliodes cinerascens cinerascens (Blanchard): Flint 1973.

Distribution.—CHILE: Curicó, Linares, Ñuble, O'Higgins, Santiago, Talca.

7. *Protochauliodes cinerascens fumipennis* Flint.
Protochauliodes cinerascens fumipennis Flint 1973.

Distribution.—CHILE: Concepción.

8. *Protochauliodes cinerascens reedi* Kimmins.
Protochauliodes reedi Kimmins 1954.
Protochauliodes cinerascens reedi Kimmins: Flint 1973.

Distribution.—CHILE: Valparaíso.

9. *Protochauliodes humeralis* (Banks).
Neohermes humeralis Banks 1908.
Protochauliodes humeralis (Banks): Weele 1910; Flint 1973.

Distribution.—CHILE: Arauco, Bío-Bío, Cautín, Concepción, Malleco, Maule.

Subfamily Corydalinae
(dobsonflies)

Genus *Chloronia* Banks 1908

10. *Chloronia absona* Flint.
Chloronia absona Flint 1992: Contreras-Ramos 1995a.

Distribution.—COSTA RICA: Alajuela, Guanacaste, Limón, San José.

11. *Chloronia antilliensis* Flint.
Chloronia antilliensis Flint 1970: Penny and Flint 1982; Contreras-Ramos 1995a.

Distribution.—DOMINICA.

12. *Chloronia banksiana* Penny and Flint.
Chloronia banksiana Penny and Flint 1982: Contreras-Ramos 1995a.
Chloronia bogotana (not Weele, misidentification): Banks 1943.

Distribution.—VENEZUELA: Aragua, Carabobo.

13. *Chloronia bogotana* Weele.
Chloronia bogotana Weele 1909: Penny and Flint 1982; Flint 1991; Contreras-Ramos 1995a.

Distribution.—BOLIVIA: La Paz; COLOMBIA: Cundinamarca; ECUADOR: Zamora-Chinchipe; PERU: Cuzco, Huánuco.

14. *Chloronia convergens* Contreras-Ramos.
Chloronia convergens Contreras-Ramos 1995a.

Distribution.—ECUADOR: Pichincha.

15. *Chloronia corripiens* (Walker).
Hermes corripiens Walker 1858.
Neuromus corripiens (Walker): MacLachlan 1869.
Neuromus winthemi Davis 1903.
Chloronia meridionalis Weele 1909.
Chloronia winthemi (Davis): Weele 1910.
Chloronia ocellaris Navás 1934a.
Chloronia corripiens (Walker): Penny and Flint 1982; Contreras-Ramos 1995a.

Distribution.—BRAZIL: Espirito Santo, Minas Gerais, Rio de Janeiro, Santa Catarina, São Paulo.

16. *Chloronia gloriosoi* Penny and Flint.
Chloronia gloriosoi Penny and Flint 1982: Flint 1992; Contreras-Ramos 1995a.

Distribution.—COSTA RICA: San José; PANAMA: Chiriquí.

17. *Chloronia hieroglyphica* (Rambur).
Neuromus hieroglyphica Rambur 1842.
Hermes hieroglyphicus (Rambur): Walker 1853.
Corydalis hieroglyphicus (Rambur): Hagen 1861.
Chloronia hieroglyphica (Rambur): Banks 1908; Penny and Flint 1982; Contreras-Ramos 1995a.

Distribution.—BRAZIL: Amazonas, Pará; FRENCH GUIANA; GUYANA; PERU: Loreto, Madre de Dios.

18. *Chloronia mexicana* Stitz.
Chloronia mexicana Stitz 1914: Penny and Flint 1982; Flint 1992; Contreras-Ramos 1995a, 1997.

Distribution.—COSTA RICA: Alajuela, Guanacaste, Heredia; GUATEMALA: Alta Verapaz, Suchitepequez; MEXICO: Chiapas, Morelos, San Luis Potosí, Tamaulipas, Veracruz.

19. *Chloronia mirifica* Navás.
Chloronia mirifica Navás 1925a: Penny and Flint 1982; Flint 1992; Contreras-Ramos 1995a, 1997.
Chloronia hieratica Navás 1928a.

Distribution.—COLOMBIA: Meta; COSTA RICA: Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José; ECUADOR: Napo, Pichincha; GUATEMALA: Alta Verapaz, Izábal, Solola; MEXICO: Oaxaca, Veracruz; PANAMA: Chiriquí, Colón; PERU: Huánuco.

20. *Chloronia osae* Flint.
Chloronia osae Flint 1992: Contreras-Ramos 1995a.

Distribution.—COSTA RICA: Puntarenas.

21. *Chloronia pallida* (Davis).
Neuromus pallidus Davis 1903.
Chloronia pallidus (Davis): Penny 1977.
Chloronia pallida (Davis): Penny and Flint 1982; Contreras-Ramos 1995a, 1997.

Distribution.—MEXICO: Chihuahua, Guerrero, Jalisco, Michoacán, Morelos, Nayarit.

22. *Chloronia plaumanni* Penny and Flint.
Chloronia plaumanni Penny and Flint 1982: Contreras-Ramos 1995a.

Distribution.—BRAZIL: Rio Grande do Sul, Santa Catarina.

23. *Chloronia zacapa* Contreras-Ramos.
Chloronia zacapa Contreras-Ramos 1995a.

Distribution.—GUATEMALA: Izábal, Zacapa.

Genus *Corydalus* Latreille 1802

24. *Corydalus affinis* Burmeister.
Corydalus affinis Burmeister 1839: Weele 1910 (in part); Penny 1977; Contreras-Ramos 1998.
Corydalus nubilus (not Erichson, misidentification): Weele 1910; Banks 1943; Penny 1982.
Corydalus sp.: Glorioso 1981.
Corydalus spec. nov.: Geijskes 1984.

Distribution.—ARGENTINA: Chaco, Misiones; BOLIVIA: Beni; BRAZIL: Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima, São Paulo; COLOMBIA: Antioquia, Boyacá, Chocó, Cundinamarca, Tolima; ECUADOR: Napo, Pichincha, Sucumbíos; FRENCH GUIANA; GUYANA; PARAGUAY; PERU: Cuzco, Loreto, Madre de Dios; VENEZUELA: Guárico.

25. *Corydalus amazonas* Contreras-Ramos.
Corydalus amazonas Contreras-Ramos 1998.

Distribution.—BRAZIL: Amazonas, Rondônia.

26. *Corydalus armatus* Hagen.
Corydalis armata Hagen 1861.
Corydalis armatus Hagen 1861.
Corydalus armatus Hagen 1861: Weele 1910 (in part); Stitz 1914 (in part); Navás 1920a, 1934a, 1935; Penny 1977 (in part), 1982 (in part); Glorioso 1981 (in part); Contreras-Ramos 1998.
Corydalis armata n. sp.: Davis 1903 (in part).
Corydalus quadrispinosus Stitz 1914.
Corydalus peruvianus (not Davis, misidentification): Banks 1943 (in part).

Distribution.—ARGENTINA: Catamarca, Jujuy, Salta, Tucumán; BOLIVIA: Chuquisaca, Cochabamba, La Paz, Santa Cruz; COLOMBIA: Boyacá, Cundinamarca, Valle del Cauca; ECUADOR: Bolívar, Chimborazo, El Oro, Esmeraldas, Imbabura, Loja, Los Ríos, Napo, Pichincha, Tungurahua, Zamora Chinchipe; PERU: Ayacucho, Cuzco, Huánuco, Junín, Lima, Pasco; VENEZUELA: Aragua, Mérida, Tachira.

27. *Corydalus arpi* Navás.
Corydalus arpi Navás 1936: Penny 1977, 1982; Contreras-Ramos 1993, 1998.

Distribution.—BRAZIL: Amazonas, Rondônia; VENEZUELA: Territorio Federal Amazonas.

28. *Corydalus australis* Contreras-Ramos.
Corydalus australis Contreras-Ramos 1998.
Corydalus affinis (not Burmeister, misidentification): Weele 1910 (in part); Penny 1977 (in part); Glorioso 1981.

Distribution.—ARGENTINA: Misiones; BRAZIL: Minas Gerais, Rio Grande do Sul, Santa Catarina; URUGUAY: Artigas.

29. *Corydalus batesii* MacLachlan.
Corydalus batesii MacLachlan 1868: Davis 1903; Geijskes 1984; Contreras-Ramos 1998.
Corydalus batesi MacLachlan: Weele 1910; Stitz 1914 (in part); Kimmins 1970; Penny 1977, 1982; Glorioso 1981.

Distribution.—BOLIVIA: Cochabamba, Santa Cruz; BRAZIL: Amazonas, Pará; COLOMBIA: Antioquia; ECUADOR: Napo; FRENCH GUIANA; GUYANA; SURINAME; PERU: Madre de Dios; VENEZUELA: Territorio Federal Amazonas.

30. *Corydalus bidenticulatus* Contreras-Ramos.
Corydalus bidenticulatus Contreras-Ramos 1998.

Corydalus lutea (not Hagen, misidentification): Glorioso 1981 (in part).
Corydalus sp. B: Contreras-Ramos 1997.

Distribution.—UNITED STATES: Arizona; MEXICO: Colima, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora.

31. *Corydalus cephalotes* Rambur.
Corydalus cephalotes Rambur 1842: Weele 1910 (in part); Stitz 1914 (in part); Penny 1977 (in part), 1982 (in part); Contreras-Ramos 1998.
Corydalis affinis (not Burmeister, misidentification): Walker 1853; Hagen 1861.
Neuromus cephalotes (Rambur): Davis 1903 (in part).
Corydalus intricatus Navás 1921: Penny 1977.

Distribution.—BRAZIL: Rio de Janeiro.

32. *Corydalus clauseni* Contreras-Ramos.
Corydalus clauseni Contreras-Ramos 1998.

Distribution.—COLOMBIA: Valle del Cauca; COSTA RICA: Heredia; ECUADOR: Cañar, Loja, Napo, Pichincha, Tungurahua.

33. *Corydalus colombianus* Contreras-Ramos.
Corydalus colombianus Contreras-Ramos 1998.
Corydalus ecuadorianus (not Banks, misidentification): Glorioso 1981 (in part).

Distribution.—COLOMBIA: Valle del Cauca.

34. *Corydalus diasi* Navás.
Corydalus diasi Navás 1915: Penny 1977; Contreras-Ramos 1998.
Corydalus finoti Navás 1921: Penny 1977.

Distribution.—ARGENTINA: Misiones, BRAZIL: Bahia, Ceará, Goiás, Minas Gerais, Rio Grande do Sul, São Paulo; PARAGUAY.

35. *Corydalus ecuadorianus* Banks.
Corydalus ecuadorianus Banks 1948: Penny 1977; Glorioso 1981 (in part); Contreras-Ramos 1998.

Distribution.—ECUADOR: Napo, Tungurahua.

36. *Corydalus flavicornis* Stitz.
Corydalus armatus flavicornis Stitz 1914: Penny 1977.
Corydalus nevermanni Navás 1934b: Penny 1977; Banks 1943.
Corydalus camposi Navás 1935: Penny 1977.
Corydalus armatus (not Hagen, misidentification): Banks 1943 (in part).
Corydalus peruvianus (not Davis, misidentification): Banks 1943 (in part).
Corydalus flavicornis Stitz: Glorioso 1981; Contreras-Ramos 1998.

Distribution.—COLOMBIA: Antioquia, Meta, Santander; COSTA RICA: Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José; ECUADOR: Guayas, Esmeraldas, Loja, Los Ríos, Napo, Pastaza, Pichincha, Tungurahua; EL SALVADOR; GUATEMALA; HONDURAS; PANAMA: Chiriquí; PERU: Huánuco, Junín, Pasco; VENEZUELA: Aragua, Bolívar, Lara, Mérida, Portuguesa, Zulia.

37. *Corydalus flinti* Contreras-Ramos.
Corydalus flinti Contreras-Ramos 1998.

Distribution.—VENEZUELA: Territorio Federal Amazonas.

38. *Corydalus hecate* MacLachlan.
Corydalis hecate MacLachlan 1866: Kimmins 1970.
Neuromus cephalotes (not Rambur, misidentification): Davis 1903 (in part).
Corydalus cephalotes (not Rambur, misidentification): Weele 1910 (in part); Stitz 1914 (in part); Penny 1977 (in part), 1982 (in part); Glorioso 1981 (in part).
Corydalus raymundoi Navás 1920b.
Corydalus sallei Navás 1920b.
Corydalus hecate MacLachlan: Contreras-Ramos 1998.

Distribution.—BRAZIL: Distrito Federal, Espirito Santo, Minas Gerais, São Paulo; PERU; VENEZUELA: Distrito Federal.

39. *Corydalus holzenthali* Contreras-Ramos.
Corydalus holzenthali Contreras-Ramos 1998.

Distribution.—BOLIVIA: Cochabamba, La Paz; PERU: Pasco.

40. *Corydalus ignotus* Contreras-Ramos.
Corydalus ignotus Contreras-Ramos 1998.

Distribution.—FRENCH GUIANA.

41. *Corydalus imperiosus* Contreras-Ramos.
Corydalus imperiosus Contreras-Ramos 1998.
Corydalus tridentatus (not Stitz, misidentification): Glorioso 1981 (in part).

Distribution.—ARGENTINA: Misiones.

42. *Corydalus longicornis* Contreras-Ramos.
Corydalus longicornis Contreras-Ramos 1998.

Distribution.—ARGENTINA: Catamarca, Salta; BOLIVIA: Chuquisaca, Cochabamba, Santa Cruz; ECUADOR: Zamora Chinchipe.

43. *Corydalus luteus* Hagen.
Corydalis lutea Hagen 1861: Davis 1903 (in part); Penny 1977 (as *nomen nudum*).
Corydalus luteus Hagen: Weele 1910 (as junior synonym of *C. cornutus* [L.]); Contreras-Ramos 1997, 1998.
Corydalus lutea Hagen: Glorioso 1981 (in part).
Corydalis crassicornis MacLachlan 1868: Davis 1903; Banks 1907; Kimmins 1970.
Corydalus crassicornis (MacLachlan): Weele 1910 (as junior synonym of *C. cornutus* [L.]).
Corydalis inamabilis MacLachlan 1868: Davis 1903; Banks 1907; Kimmins 1970.
Corydalus inamabilis (MacLachlan): Weele 1910 (as junior synonym of *C. cornutus* [L.]).
Corydalus armatus laevicornis Stitz 1914: Penny 1977.

Distribution.—BELIZE; COSTA RICA: Alajuela, Guanacaste, Heredia, Limón, Puntarenas, San José; EL SALVADOR; UNITED STATES: Texas; GUATEMALA: Alta Verapaz, Chiquimula, Escuintla, Guatemala, Sacatepéquez, San Marcos, Santa Rosa, Suchitepequez, Zacapa; HONDURAS; MEXICO: Chiapas, Coahuila, Hidalgo, Nuevo León, Oaxaca, Querétaro, San Luis Potosí, Tabasco, Tamaulipas, Veracruz; NICARAGUA; PANAMA: Zona del Canal, Chiriquí, Colón.

44. *Corydalus magnus* Contreras-Ramos.
Corydalus magnus Contreras-Ramos 1998.
Corydalus lutea (not Hagen, misidentification): Glorioso 1981 (in part).
Corydalus sp. M: Contreras-Ramos 1997.

Distribution.—COSTA RICA: Alajuela, Guanacaste, Puntarenas; EL SALVADOR; GUATEMALA: Alta Verapaz, Baja Verapaz, Suchitepequez; MEXICO: Chiapas, Puebla, San Luis Potosí, Veracruz.

45. *Corydalus neblinensis* Contreras-Ramos.
Corydalus neblinensis Contreras-Ramos 1998.

Distribution.—VENEZUELA: Territorio Federal Amazonas.

46. *Corydalus nubilus* Erichson.
Corydalis nubila Erichson 1848: Hagen 1861 (in part); Davis 1903 (in part).
Corydalus nubilus Erichson: Stitz 1914; Penny 1977 (in part); Glorioso 1981; Geijskes 1984; Contreras-Ramos 1998.
Corydalus nevermanni (not Navás, misidentification): Penny 1982.
Corydalus titschacki Navás 1928b: Penny 1977.

Distribution.—BRAZIL: Amazonas, Pará, Roraima; FRENCH GUIANA; GUYANA; VENEZUELA: Territorio Federal Amazonas.

47. *Corydalus parvus* Stitz.

Corydalus parvus Stitz 1914: Penny 1977; Contreras-Ramos 1998.
Corydalus armatus (not Hagen, misidentification): Glorioso 1981 (in part).

Distribution.—ECUADOR: Pastaza, Zamora Chinchipe; PERU: Cuzco, Huánuco, Pasco.

48. *Corydalus peruvianus* Davis.
Corydalis peruviana Davis 1903.
Corydalus armatus (not Hagen, misidentification): Weele 1910 (in part); Stitz 1914 (in part); Penny 1977 (in part), 1982 (in part); Glorioso 1981 (in part).
Corydalis crassicornis (not MacLachlan, misidentification): Banks 1914.
Corydalus primitivus fera Navás 1927: Penny 1977.
Corydalus peruvianus Davis: Banks 1943 (in part); Contreras-Ramos 1997, 1998.

Distribution.—ARGENTINA: Jujuy, Salta, Tucumán; BOLIVIA: Chuquisaca, Cochabamba, La Paz, Tarija; COLOMBIA: Antioquia, Cundinamarca, Meta, Putumayo, Valle del Cauca; COSTA RICA: Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José; ECUADOR: Cotopaxi, Guayas, Los Ríos, Morona Santiago, Napo, Pastaza; Pichincha; Sucumbíos; GUATEMALA: Escuintla, Izábal, Quiché, San Marcos; MEXICO: Chiapas, Oaxaca, Puebla, Tabasco, Veracruz; PANAMA: Bocas del Toro, Chiriquí, Colón, Darién; PERU: Amazonas, Huánuco, La Libertad, Pasco; VENEZUELA: Aragua, Barinas, Distrito Federal, Mérida.

49. *Corydalus primitivus* Weele.
Corydalus primitivus Weele 1909: Weele 1910 (in part); Stitz 1914; Navás 1929; Penny 1977, 1982 (in part); Glorioso 1981 (in part), Contreras-Ramos 1998.

Distribution.—ARGENTINA: Catamarca, Jujuy, Salta, Tucumán; BOLIVIA: Santa Cruz.

50. *Corydalus tesselatus* Stitz.
Corydalus batesi tesselatus Stitz 1914.
Corydalis nubila (not Erichson, misidentification): Hagen 1861 (in part); Davis 1903 (in part); Banks 1943.
Corydalus bolivari Banks 1943: Glorioso 1981; Contreras-Ramos 1993.
Corydalus tesselatus Stitz: Penny 1977 (incorrect locality); Contreras-Ramos 1998.

Distribution.—COLOMBIA; VENEZUELA: Aragua, Distrito Federal, Mérida, Tachira.

51. *Corydalus texanus* Banks.
Corydalis texana Banks 1903a: Penny 1977 (as junior synonym of *C. cornutus* [L.]).
Corydalis cognata (not Hagen, misidentification): Banks 1892, 1903b, 1907; Davis 1903; Chandler 1956.
Neuromus pallidus (not Davis): Davis 1903 (mislabeled photograph).
Corydalus pallidus (not Davis): Weele 1910 (invalid combination based on mislabeled photograph; as junior synonym of *C. cornutus* [L.]).
Corydalus cognatus (not Hagen, misidentification): Weele 1910 (in part; as junior synonym of *C. cornutus* [L.]); Evans 1972 (in part).
Corydalus texanus Banks: Weele 1910 (as junior synonym of *C. cornutus* [L.]); Contreras-Ramos 1997, 1998.
Corydalus cornutus (not Linnaeus, misidentification): Stitz 1914 (in part); Glorioso 1981 (in part); Hermann and Davis 1991.
Corydalus similis Stitz 1914: Banks 1943 (misidentification); Penny 1977 (in part).
Corydalus constellatus Navás 1934b: Penny 1977.

Distribution.—UNITED STATES: Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah; GUATEMALA: Baja Verapaz, Chiquimula; MEXICO: Baja California, Baja California Sur, Chiapas, Chihuahua, Colima, Distrito Federal, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora, Veracruz.

52. *Corydalus tridentatus* Stitz.
Corydalus tridentatus Stitz 1914: Penny

1977; Glorioso 1981 (in part); Contreras-Ramos 1998.
Corydalus tridentatus nigripes Stitz 1914.

Distribution.—BRAZIL: Espirito Santo. Paraná, Rio Grande do Sul.

Corydalus sp. 1.
Corydalus sp. 1 (near *C. affinis* Burmeister): Contreras-Ramos 1998.

Distribution.—BRAZIL: São Paulo: São José dos Campos.

Corydalus sp. 2
Corydalus tesselatus (not Stitz, misidentification): Banks 1943.
Corydalus ecuadorianus (not Banks, misidentification): Glorioso 1981 (in part).
Corydalus sp. 2 (near *C. ecuadorianus* Banks): Contreras-Ramos 1998.

Distribution.—COLOMBIA: [Cundinamarca?]: St. [San] Antonio, 2000 m.

Corydalus sp. 3.
Corydalus sp. 3 (near *C. nubilus* Erichson): Contreras-Ramos 1998.

Distribution.—VENEZUELA: Bolívar: Ciudad Bolívar.

Corydalus sp. 4.
Corydalus sp. 4 (near *C. tesselatus* Stitz): Contreras-Ramos 1998.

Distribution.—ECUADOR: Sucumbíos: El Reventador, [aprox. 900 m].

Corydalus sp. 5.
Corydalus sp. 5 (near *C. colombianus* Contreras-Ramos): Contreras-Ramos 1998.

Distribution.—ECUADOR: Pichincha: Palmeras.

Genus *Platyneuromus* Weele 1909

53. *Platyneuromus honduranus* Navás.
Platyneuromus soror hondurana Navás 1928b.
Platyneuromus auritus Kimmins 1928.
Platyneuromus honduranus Navás: Glorioso and Flint 1984; Contreras-Ramos 1997.

Distribution.—GUATEMALA: Alta Verapaz, El Petén, Izábal; HONDURAS: Atlántida, Cortés; MEXICO: Chiapas.

54. *Platyneuromus reflexus* Glorioso and Flint.
Platyneuromus reflexus Glorioso and Flint 1984: Contreras-Ramos 1997.

Distribution.—GUATEMALA: Alta Verapaz; MEXICO: Chiapas.

55. *Platyneuromus soror* (Hagen).
Corydalis soror Hagen 1861.
Neuromus soror (Hagen): Davis 1903.
Neuromus (*Chloronia*) *soror* (Hagen): Banks 1908.
Platyneuromus soror (Hagen): Weele 1909, 1910; Stitz 1914; Penny 1977; Glorioso 1981; Glorioso and Flint 1984; Contreras-Ramos 1991b, 1997; Contreras-Ramos and Harris 1998.
Doeringia christel Navás 1925b.

Distribution.—COSTA RICA: Alajuela, Cartago, Guanacaste, Heredia, Puntarenas, San José; MEXICO: Chiapas, Distrito Federal, Hidalgo, Estado de México, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz; PANAMA: Chiriquí.

Platyneuromus sp.
Platyneuromus larval form A: Contreras-Ramos and Harris 1998.

Distribution.—MEXICO: Guerrero: 56 km NE Atoyac on road to Puerto del Gallo, 17.417°N, 100.217°W, 1372 m; Sinaloa: 4.83 km W Palmito.

Family Sialidae
(alderflies)

Genus *Protosialis* Weele 1909

56. *Protosialis bifasciata* (Hagen).
Sialis bifasciata Hagen 1861: Davis 1903.
Protosialis bifasciata (Hagen): Weele 1910; Penny 1977.

Distribution.—CUBA.

57. *Protosialis bimaculata* Banks.

Protosialis bimaculata Banks 1920: Penny 1977, 1981 [1982].

Distribution.—BOLIVIA: La Paz.

58. *Protosialis brasiliensis* Navás.
Protosialis brasiliensis Navás 1936: Penny 1977, 1981 [1982].

Distribution.—BRAZIL: São Paulo.

59. *Protosialis chilensis* (MacLachlan).
Sialis chilensis MacLachlan 1870: Davis 1903; Flint 1973.
Protosialis chilensis (MacLachlan): Weele 1910; Penny 1977.

Distribution.—CHILE: Arauco, Concepción, Llanquihue, Malleco, O'Higgins, Talca, Valdivia.

60. *Protosialis flammata* Penny.
Protosialis flamatta Penny 1981 [1982].

Distribution.—BRAZIL: Amazonas.

61. *Protosialis flavicollis* (Enderlein).
Sialis flavicollis Enderlein 1910.
Protosialis flavicollis (Enderlein): Penny 1977, 1981 [1982].

Distribution.—COLOMBIA: Tolima.

62. *Protosialis mexicana* (Banks).
Sialis mexicana Banks 1901: Henry et al. 1992.
Protosialis mexicana (Banks): Weele 1910; Penny 1977, E. D. Evans (*in litt.*); Contreras-Ramos 1991a.

Distribution.—MEXICO: Chiapas, Veracruz; PANAMA.

63. *Protosialis nubila* Navás.
Protosialis nubila Navás 1933: Penny 1977, 1981 [1982].

Distribution.—BRAZIL: Matto Grosso?

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IDENTITY OF *SYRISTA SPECIOSA* MOCSÁRY AND NOTES ON THE GENUS *UROSYRISTA* MAA (HYMENOPTERA: CEPHIDAE)

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Abstract.—The holotype of *Syrista speciosa* Mocsáry, described from Vietnam, is redescribed and illustrated and confirmed as belonging to the genus *Urosyrista* Maa. Possible characters are presented to separate it from other species of this southeastern Asian genus.

Key Words: Cephidae, *Urosyrista,* stem sawflies

In the treatments of world Cephidae (Benson 1946, Muche 1981) and Asian Cephidae (Maa 1944, 1949), the species described as *Syrista speciosa* by Mocsáry (1904), an unusually large and colorful cephid from "Tonkin," has never been studied and confidently placed. Benson (1946) placed *S. speciosa* in his new genus *Cephalocephus,* qualifying it with the statement that "it seems almost certain" that it belongs to this genus. Maa (1949) synonymized *Cephalocephus* with *Urosyrista* which he had described earlier (Maa 1944). Although Maa (1949) did not see *Cephalocephus xanthus* Benson, the type species of *Cephalocephus,* both generic descriptions are almost identical and their synonymy cannot be disputed. Maa (1949) did not mention *S. speciosa* or put it in his key to species of *Urosyrista.* Muche (1981), who based much of his work on the literature, placed *S. speciosa* in *Urosyrista* but did not include it in his key to *Urosyrista* species, which was taken directly from Maa (1949).

Here, I redescribe, illustrate, and confirm the generic placement of *Syrista speciosa* based on examination of the holotype.

Urosyrista speciosa (Mocsáry)
(Figs. 1–9)

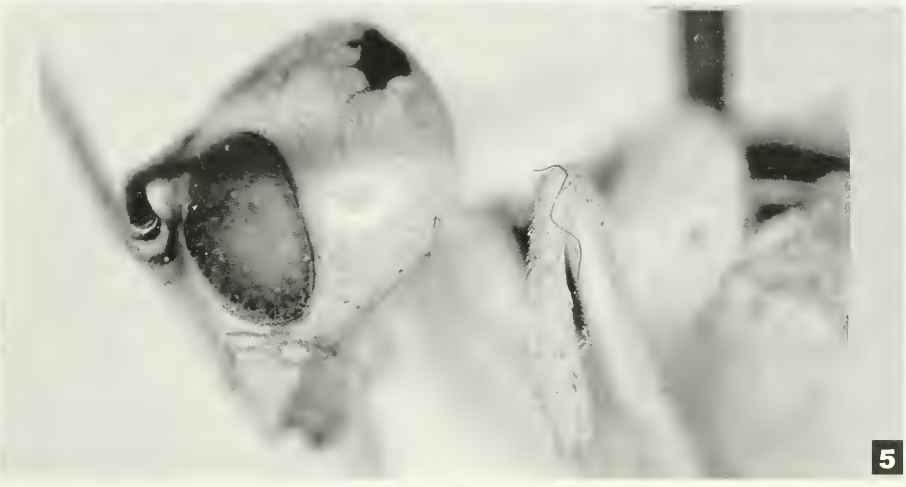
Syrista speciosa Mocsáry 1904: 496. Female. "Tonkin: Montes Mauson, in altitudine 2–3,000 pedum a H. Fruhstorfer detecta. (Mus. Hung.)."

Cephalocephus speciosa: Benson 1946: 100.

Urosyrista speciosa: Muche 1981: 265.

Description.—Length, 16 mm. Head and body smooth, shining, without punctures. *Color:* Yellowish with black markings (as shown in Figs. 1–9); antenna pale yellowish ventrally, black dorsally, with basal 3 segments black. Wings hyaline, apices slightly blackish; most of stigma black, and veins dark brown, costa and margins of stigma yellowish. *Head*: In dorsal view, enlarged and swollen behind eyes, elongated, 1.2× broader than long, distance behind eyes 1.3× eye length; distance from front ocellus to hind margin of head 3× distance from front ocellus to antennal sockets. Antennal-tentorial distance 2× distance between antennae. Antenna 30-segmented. Left mandible bidentate, subapical tooth slightly longer and stouter than apical tooth, without

Figs. 1–3. *Urosyrista speciosa*. 1, Lateral view. 2, Dorsal view. 3, Dorsal view of thorax.



Figs. 4–6. *Urosyrista speciosa.* 4, Head, front view. 5, Head, lateral view. 6, Head, dorsal view.

Figs. 7–9. *Urosyrista speciosa*. 7, Thorax, lateral view. 8, Apex of abdomen and sheath, lateral view. 9, Apex of abdomen and sheath, dorsal view.

intermediary tooth (Fig. 4). Sixth segment of maxillary palpus originating from near apex of 5th segment; segment 4 about 1.5× length of segment 6. *Thorax:* Forewing with anal crossvein. Hindwing with cubital cell. Hindtibia with 2 preapical spines. Midtibia with one preapical spine. Hindbasitarsus subequal in length to remaining tarsal segments combined. Tarsal claws bifid, inner tooth about as long as outer tooth, with-

out basal lobe. *Abdomen:* Cercus less than half length of sawsheath (Figs. 8, 9). Sheath as in Figs. 8, 9; in dorsal view, thick and parallel sided; length about .6× length of basal plate and slightly less than half as long as hind basitarsus.

Holotype.—Female, labeled "Tonkin, Montes Manson, April, Mai, 2–3,000′, H. Fruhstorfer," "Typus 1904 Syrista speciosa Mocs." (red label). The third label on the pin is a blank red label. In the Hungarian Natural History Museum, Budapest.

Discussion.—Almost all characters of *Syrista speciosa* are consistent with *Urosyrista,* and placement in this genus is correct according to generic definitions and keys by Maa (1944, 1949), Benson (1946), and Muche (1981). Some minor differences are the lack of a basal swelling on the tarsal claws (according to Benson 1946 the claws have a small basal swelling) and the subapical tooth of the left mandible which, although longer than the apical tooth, is not as large in relation to the apical tooth as figured by Benson (1946, fig. 13). Unique characters for *Urosyrista* in the Cephidae are the enlarged head behind the eyes (Figs. 5, 6), the lack of an intermediate tooth and large innter tooth of the left mandible (Fig. 4), the apical segment of the maxillary palpus emerging from near the apex of the fifth segment, and the bifid tarsal claws, lacking a basal lobe.

Urosyrista is known only from southeastern Asia, and three species are currently included: *U. speciosa* (Mocsáry) from Vietnam; *U. montana* (Maa) (= *Cephalocephus xanthus Benson* according to Maa 1949) from China and Burma; and *U. mencioyana* Maa from China. Maa (1949) considered three color forms of *U. mencioyana,* the typical form, var. *unicolor* Maa, and var. *xanthobalteata* Maa. All three are separated by the amount of black on the pronotum. The host plant is known only for *U. mencioyana*; specimens were reared from *Acanthopanax trifoliatus* (Lour.) Merr. (Araliaceae) (Maa 1944).

Urosyrista speciosa appears to be most similar to *U. montana* because they share the thick, parallel sided sheath in dorsal view. The sheath of *U. mencioyana* is slender and gradually tapering toward its apex. I hesitate to use coloration. In species as these with numerous black markings, variation in the amount of black can be extensive. Maa (1949) has alluded to this by separating several color forms of *U. mencioyana.* However, as it may be useful, *U. speciosa* is more extensively yellow than the other two species and the antennae are black dorsally, pale whitish ventrally, with the basal three segment entirely black. *Urosyrista montana* has the antennae apically dull brown to black, basally distinctly paler, and the mesepisternum mostly black with a median yellow band. *Urosyrista mencioyana* has the antennae apically yellow, basally distinctly darker, and the head and thorax mostly black.

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FRANKLINIELLA ZUCCHINI (THYSANOPTERA: THRIPIDAE), A NEW SPECIES AND VECTOR OF TOSPOVIRUS IN BRAZIL

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Abstract.—***Frankliniella zucchini,* new species,** is described. It is a vector of a tospovirus that causes zucchini lethal chlorotic disease of *Cucurbita pepo* L. cv. Caserta in São Paulo State, Brazil.

Key Words: *Frankliniella zucchini* n. sp., Thysanoptera, Thripidae, zucchini, vector, ZLCV, Brazil

A serious disease of zucchini squash, *Cucurbita pepo* L. cv. Caserta, currently known as zucchini lethal chlorotic disease (ZLC), was discovered during 1995 in experimental fields at Piracicaba, São Paulo State, Brazil (Rezende et al. 1997). This disease is caused by a species of *Tospovirus*, zucchini lethal chlorotic virus (ZLCV) (Pozzer et al. 1996). Tospoviruses can be transmitted only by thrips adults and larvae. The disease apparently was present sporadically in the state prior to 1991 when many zucchini plants were observed with symptoms of ZLC in Campinas county. Since then, symptoms of ZLC were observed more frequently on zucchini squash and watermelon. *Frankliniella zucchini,* new species, described here was the predominant thrips species collected from foliage and flowers of infected plants in Piracicaba. In preliminary transmission tests, this thrips was found to be a vector of ZLCV to zucchini seedlings (Rezende 1998, personal communication).

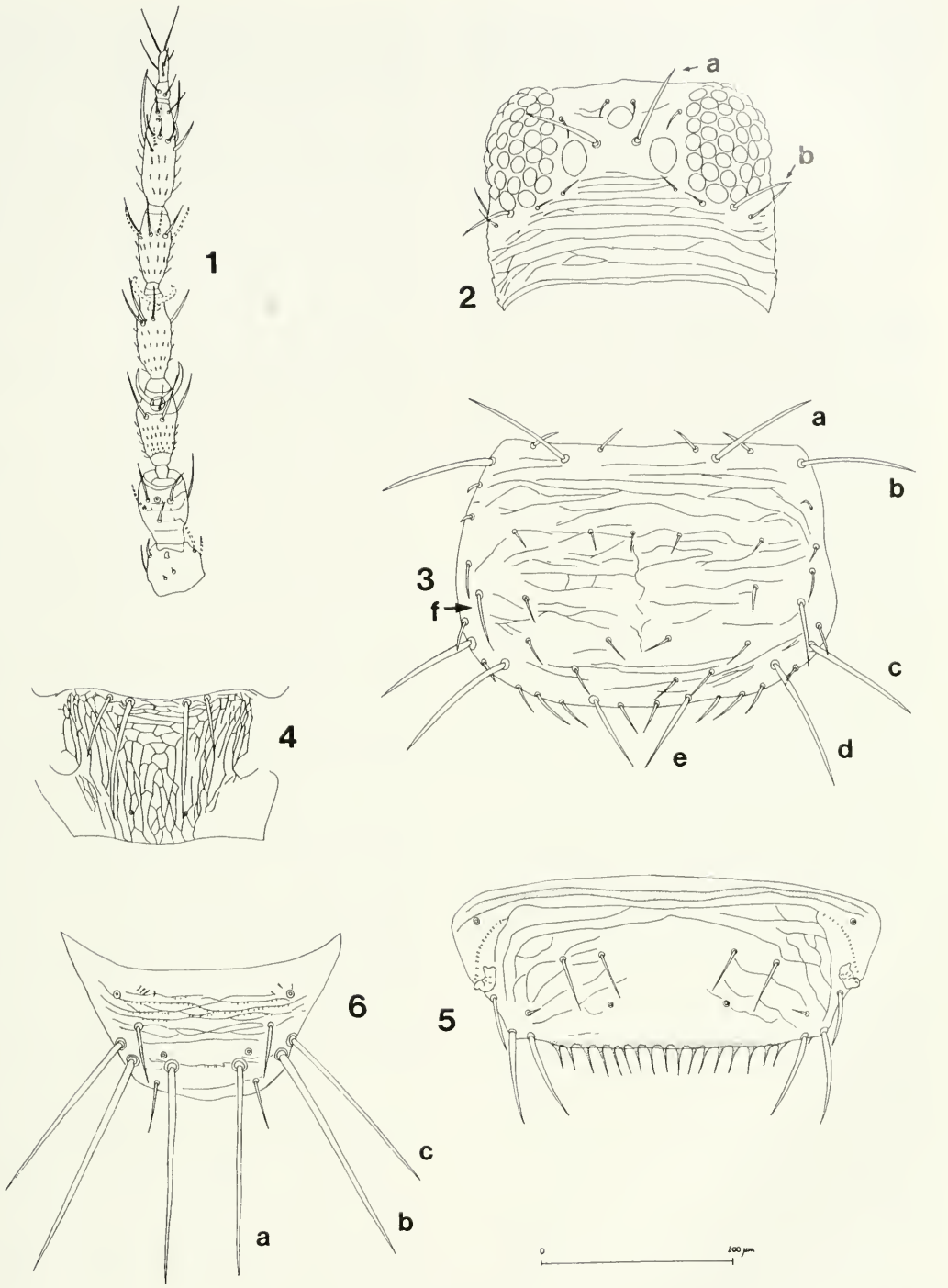
Two polyphagous *Frankliniella* species are vectors of "tomato spotted wilt virus" (TSWV) and "tomato chlorotic spot virus" (TCSV) in Brazil (Wijkamp et al. 1995). *Frankliniella schultzei* (Trybom) dark form is an efficient vector of TSWV and TCSV that damages tomato crops. Although the yellow form of this species was previously not considered to be a vector, it is an inefficient vector of TSWV according to Wijkamp et al. (1995). The recently established *F. occidentalis* (Pergande) is a pest of various agricultural crops and also a vector. *Frankliniella zucchini* is known to vector only ZLCV and is the fifth *Frankliniella* species to be implicated in the transmission of tospoviruses. The other two are *F. fusca* (Hinds) and *F. intonsa* (Trybom).

For measurements and counts, the values for the holotype are given first and are followed by values for the paratypes in parentheses. If parentheses are absent the values are either for the holotype or for all measured specimens.

Frankliniella zucchini Nakahara and Monteiro, new species

(Figs. 1–6)

Female (macropterous).—Body generally yellow; forewing pale yellow, legs paler



Figs. 1–6. *Frankliniella zucchini*. Female. 1, Right antenna. 2, Head (a, ocellar seta III; b, POiv seta). 3, Pronotum (a, anteromarginal seta; b, anteroangular setae; c, outer posteroangular seta; d, inner posteroangular seta, e. posteromarginal seta II; f, submarginal seta). 4, Metanotum. 5, Abdominal tergite VIII. 6, Abdominal tergite IX (a, B1seta; b, B2 seta; c, B3 seta). Scale = 0.1 mm.

yellow than body; body and forewing setae brown. Antennal segment I as pale as head; segment II pale yellow in proximal ½, shaded light brown distally; segment III pale yellow in proximal ⅔ including pedicel, distally brown; segment IV pale yellow in proximal ½, brown distally and in pedicel; segment V pale yellow in proximal ⅓, distally brown; segments VI to VIII brown.

Antenna (Fig. 1): More than twice as long as head; pedicel of segment III with slight angulation, segments III and IV each with v-shaped forked sense cones, 22–27 μ long; segment III distad of subapical setae slightly converging to apex, about ¼ length of segment, segment IV constricted into a neck in distal part; segment VI slightly pedicellate at base, inner sense cone 32–35 μ long, extending distally at least to apex of segment VII.

Head (Fig. 2): Slightly shorter than pronotum, about 1.5 times wider than long, cheeks rather straight, compound eyes almost twice as long as occiput; interocellar area without sculpturing, caudad of compound eyes with transverse striae, those more posterior spaced farther apart. Compound eyes each with 4 pigmented facets in 1–2,3,5 pattern (see Nakahara 1988). Diameter of fore ocellus 15–17 μ. Ocellar setae I short, about 12 μ long, just anterior of fore ocellus; ocellar setae II short, laterad of fore ocellus and just mesad of inner margin of compound eye, about 12 μ long; ocellar setae III well developed (Fig. 2a), between anterior part of posterior ocelli, separated by about diameter of fore ocellus, 45(37–48) μ long. Postocular (PO) setae 5 pairs; POi seta absent; POii seta 12–15 μ long, caudad of posterior ocellus; next laterad POiii seta 10–12 μ long; POiv seta longest (Fig. 2b), 32(24–33) μ long; POv and POvi setae laterad of and shorter than seta iv but longer than setae ii and iii. Mouthcone conical, longer than head, distal ⅖ less convergent than basal ⅗, extending to posterior margin of prosternum; mandible 124–136 μ long.

Pronotum (Fig. 3): Rectangular, broader than long, sculptured with irregularly spaced transverse striae and sparsely anastomosing. Median discal area with 3–5 setae 10–12 μ long; 2 irregular rows of discal setae in posterior ⅓, 7–9 setae in anterior row including a pair of longer submarginal setae (Fig. 3f), 20–24 μ, anterior of posteroangular setae; posterior row normally with 4 setae; anteromarginal setae 37–42(42–48) μ long (Fig. 3a), 2 short setae, 10–12 μ long, between anteromarginal setae; anteroangular setae 48(48–59) μ long (Fig. 3b); posteroangular seta inner pair 59 (57–67) μ long (Fig. 3d), outer pair 57–59(59–64) μ long (Fig. 3c), about ½ as long as notum; posteromarginal seta II 32(32–40) μ long (Fig. 3e). *Mesonotum:* Subtrapezoidal, anterior angulate area smooth with pair of campaniform sensilla, median and posterior parts transversely sculptured, laterally with striae oriented longitudinally; 2 pairs of short setae on or near posterior margin, inner pair 17–20 μ long, outer pair slightly stouter, 20–24 μ long. *Metanotum* (Fig. 4): Reticulated with most reticles longer than wide and oriented longitudinally, reticles in anterior medial area more polygonal and wider than other reticles; median setae 55–59(54–59) μ long, thicker than lateral setae 35–37(35–37) μ long; 2 campaniform sensilla in posterior ⅓ of notum.

Forewing: Rather straight, apex pointed; fringe cilia wavy; costa with 20–24(19–20) cilia, 23–24(22–24) setae, setae at midlength 40(37–42) μ long, shorter than width of forewing; forevein with 19–21(18–20) setae, hindvein with 16–17(14–15) setae; scale with 4 marginal and 1 discal setae.

Abdomen: Tergites sculptured anteriorly, and laterally of median setae and campaniform sensilla; median setae short, on VII 17–20 μ long; short ctenidia on tergite IV; posterior margins of intermediate tergites with series of low, truncate lobes, with a few small teeth laterally; tergite VIII with posteromarginal comb complete with 14(13–17) microtrichia, longest 17–20 μ long (Fig. 5); tergite IX with microtrichia on anastomosing striae, posterior pair of

campaniform sensilla near B1 setae (Fig. 6); tergite X subequal to IX, dorsal split almost complete on X. Ovipositor well developed, 183(222–235) μ long.

Measurements: Female holotype and (paratypes) in μ. Body length from anterior of eye 1176(1161–1221), distended 1423(1408–1568). Antenna: Total length 270(265–280); length and width of segment I 24(24), 27(27–30); II 37(35–37), 24(27); III 50(48–50), 22(22); IV 45(42–48), 20(20–21); V 37(37–40), 17(17(20); VI 52(52–54), 18(17–20); VII 10(10–11), 7(7); VIII 15(15), 5(5–6). Head length from anterior of compound eye 100(96–106), width at compound eyes 151(148–156), width at cheeks 156(143–158); length of compound eye 62(62–69), width 45; length of occiput posterior of compound eye 37(35–37). Pronotal length 124(126–133), width 190(178–190). Forewing length 729(679–729), width at midlength 57(52–57). Length of abdominal tergite IX 62(64–67), length of B1 setae 104–109(96–109) (Fig. 6a), B2 setae 101–106 (104–109) (Fig. 6b), B3 seta 100(100) (Fig. 6c); length of tergite X 64(64–67), length of B1 seta 109(96–111), B2 seta 98(94).

Male (macropterous).—Smaller than female, otherwise similar in color and most anatomical structures. Body length 1,000–1,050 μ. Antennal length 220–246 μ. Abdominal tergite VIII with complete posteromarginal comb with 13–14 long, slender microtrichia; sternites III-VII each with transversve glandular area with anterior and posterior margins concave, on III 52–62 μ wide, 15–17 μ long, on VII 40–54 μ wide, 12–15 μ long, 0.30–0.38 as wide as sternite; sternite VIII with posteromarginal microtrichia.

Type material.—Holotype ♀ and 18 ♀ and 2 ♂ paratypes: Brasil, São Paulo, Piracicaba, *Cucurbita pepo* L, cv. Caserta, 14-VII-95. R.C. Monteiro. Holotype and 10 paratypes deposited in Departamento de Entomologia, ESALQ, Universidade de São Paulo, Piracicaba, Brazil, 10 paratypes in the National Museum of Natural History, Smithsonian Institution, Washington D.C, and 3 paratypes in The Natural History Museum, London, United Kingdom.

Etymology.—The species is named after the common name of the host, "zucchini," and is a noun in apposition.

Distribution.—Known only from São Paulo State, Brazil.

Collected from.—*Cucurbita pepo* L. cv. Caserta (zucchini).

Comments.—*Frankliniella gemina* Bagnall and *F. rodeos* Moulton in Brazil are similar to *F. zucchini* in color and most anatomical characters. *Frankliniella zucchini* lacks POi seta and has ocellar setae III positioned between the anterior part of posterior ocelli and separated by about the width of the fore ocellus; whereas POi setae are present in the other two species and ocellar setae III are aligned with the anterior margin of posterior ocelli or slightly anterior and are farther apart.

Most *Frankliniella* species have three pairs of short postocular (PO) setae mesad or anteromesad of the fourth or longest pair of PO setae which is positioned posterior of the compound eye (Fig. 2). When only two pairs of short PO setae are present, the POi seta is normally absent. The normal position of POi seta is caudad of and usually slightly mesad of the inner margin of the posterior ocelli.

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THE LARVA OF *CHALCIDOMORPHINA AURATA* ENDERLEIN 1914 (DIPTERA: STRATIOMYIDAE) FROM "ILHA DE MARAMBAIA," RIO DE JANEIRO, BRAZIL

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Abstract.—The larva of *Chalcidomorphina aurata* is described for the first time, based on six larvae and the puparium. Larvae were collected under the bark of fallen trees in a tropical rain forest at Ilha da Marambaia, State of Rio de Janeiro, Brazil (23°04′S, 43°53′W, approximately 42 km^2). Some biological notes are also presented.

Key Words: Stratiomyidae, Pachygastrinae, *Chalcidomorphina aurata,* soldier-flies, larvae, tropical rain forest

The pachygastrine genus *Chalcidomorphina* Enderlein, 1914, with four species, is widespread in the Neotropics, from Mexico to Brazil: *Chalcidomorphina aurata* Enderlein, 1914 (Mexico, Panama, Colombia, Peru and Brazil); *C. plana* James, 1967 (Dominica); *C. terataspis* James, 1974 (Peru); and *C. argentea* McFadden, 1980 *in* James et al., 1980 (Mexico) (James 1973, James et al. 1980).

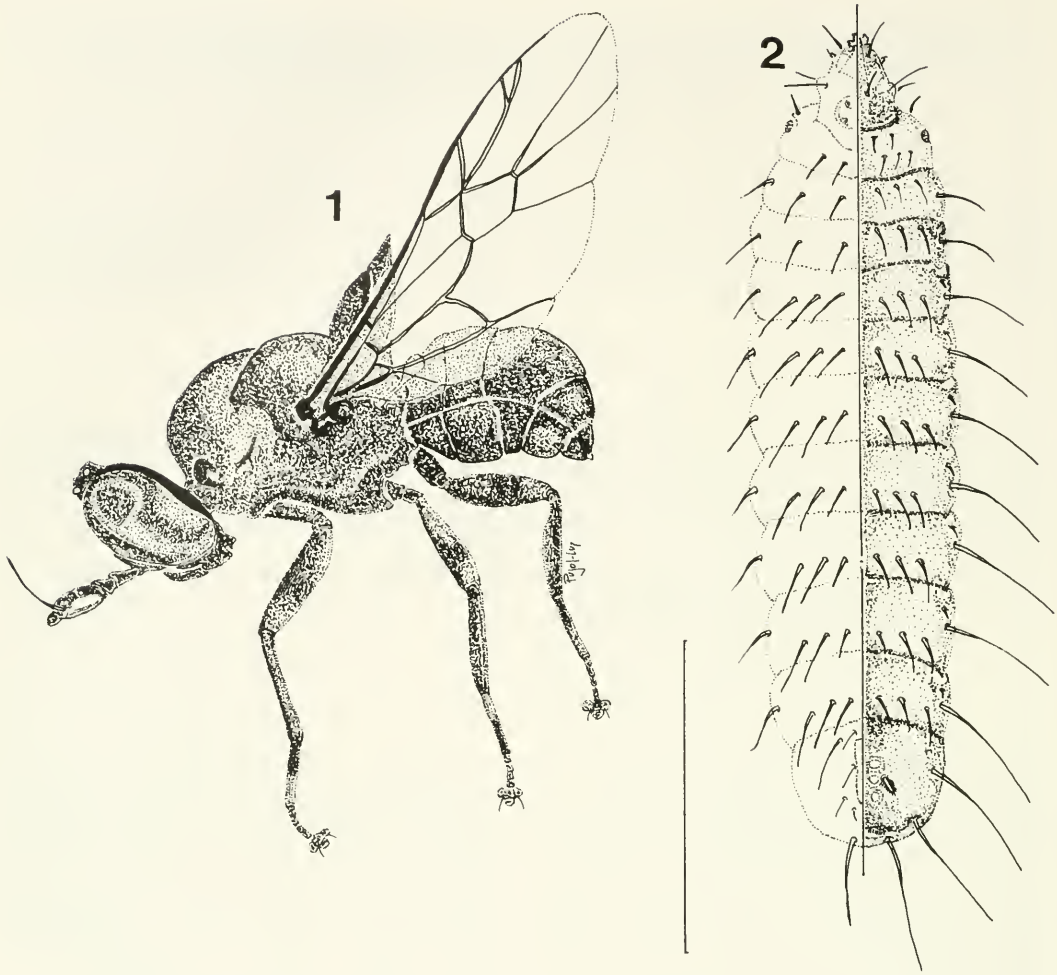
James (1974) recognized *Chalcidomorphina* based on the following characters: (1) antenna elongate, with long scape and flagellum, and (2) scutellum projected into an elongate, spur-like process (Fig. 1). James (1974) segregated *Chalcidomorphina* and *Dactylacantha* Lindner, 1964, from the related genus *Dactylodeictes* Kertész, 1914, based on wing venation.

Pachygastrinae larvae from the Neotropics have never been described. McFadden (1967) and James (1981) furnished the last records of the known North American larvae of this subfamily. They studied Nearctic representatives of some genera that are widespread over much of the Americas (e.g., *Eidalimus* Kertész, 1914 [=*Eucynipimorpha* Malloch, 1915; =*Eupachygaster* authors, part, not Kertész, 1911]; *Gowdeyana* Curran, 1928 [=*Eupachygaster* authors, part, not Kertész, 1911; =*Paraeidalimus* Lindner, 1964] and *Zabrachia* Coquillett, 1901) (James et al. 1980).

Here we describe the larva of *Chalcidomorphina aurata* for the first time, based on six larvae and the puparium. Some of the larval features employed in this work are the same used by McFadden (1967) and James (1981) to describe other genera.

Chalcidomorphina larvae were collected under the bark of fallen trees in a tropical rain forest at Ilha da Marambaia, State of Rio de Janeiro, Brazil, (23°04′S, 43°53′W, approximately 42 km^2) outside and inside the forest behind a dam (a restricted area of the Brazilian Navy).

The junior author collected approximately 35 to 50 larvae of different instars at each site belonging to two genera, *Chalcidomorphina* and *Cyphomyia* Wiedemann, 1819 (Clitellariinae). Field and laboratory



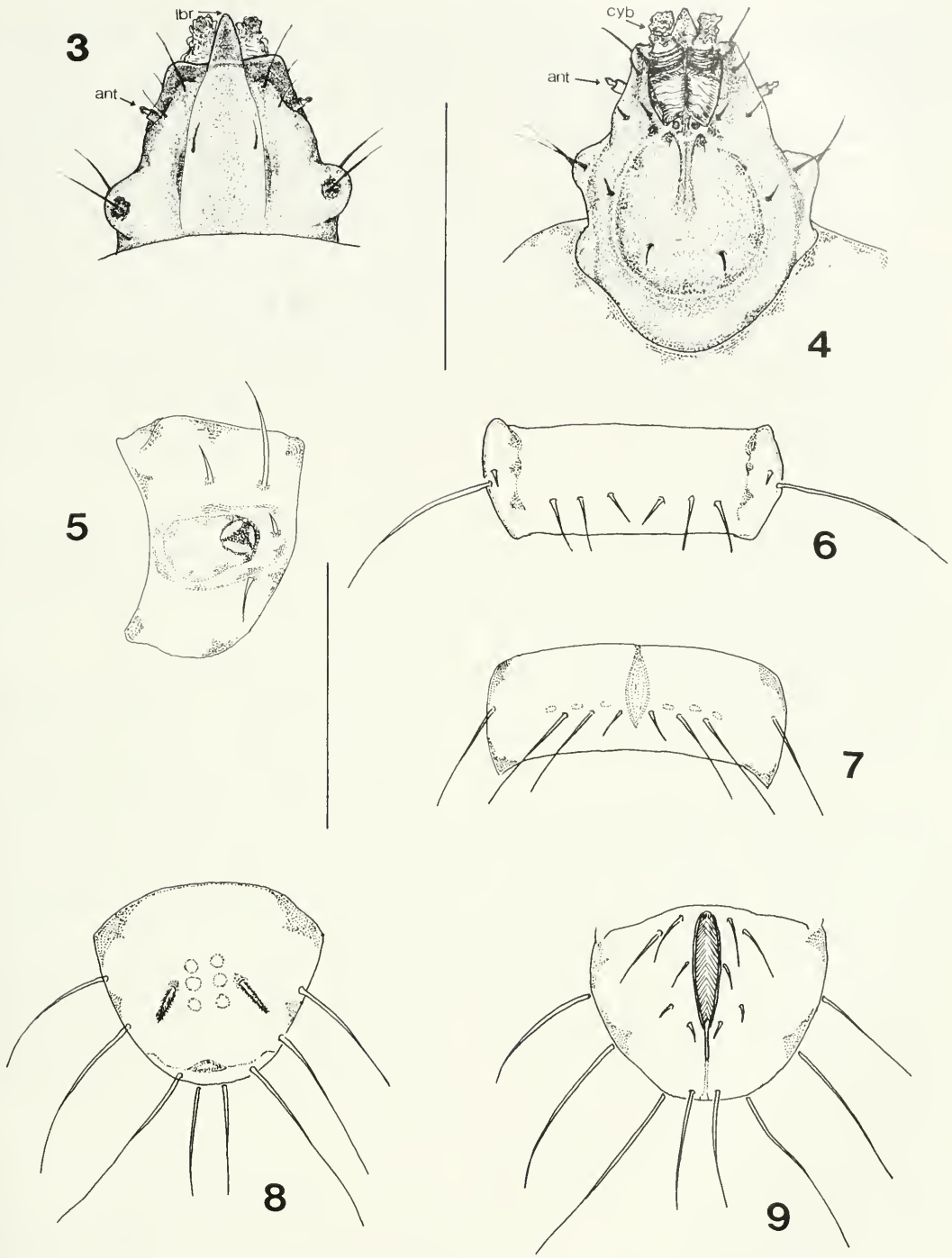
Figs. 1–2. *Chalcidomorphina aurata*. 1, Female habitus (all pilosity is omitted). 2, Larva (right in dorsal view; left in ventral view). Scale line = 2.0 mm.

observations suggest that larvae of *C. aurata* feed on microorganisms occurring in the moist areas beneath the bark of trees. The trees where the larvae were found were not identified. We also confirm McFadden's (1967) statement concerning the gregarious behavior of larvae of pachygastrine soldierflies.

The larvae of *C. aurata* were reared in semi-natural conditions, segregated by size classes, and put on individual petri dishes having as substrate the same moist substance present where the larvae were living. A single female was collected flying over a tree. We believe that oviposition occurs in the moist substrate, through crevices in the bark, because a large number of the smallest larvae of *C. aurata* were found there.

The females that emerged are extremely similar to those described by Lindner (1951), James (1974) and James et al. (1980), but showed a chromatic pattern of the eyes not described by these authors. The eyes in living insects are brownish with a greenish "9-shaped" pattern in lateral view (Fig. 1).

The terminology adopted in the descriptions follows James (1981) and Rozkošný



Figs. 3–9. Larva of *Chalcidomorphina aurata*. 3, Head, dorsal view. 4, Head, ventral view. 5, Right spiracle, lateral view. 6, Abdominal segment 6, dorsal view. 7, Abdominal segment 6, ventral view. 8, Abdominal segment 8, dorsal view. 9, Abdominal segment 8, ventral view. Scale lines = 0.5 mm (Figs. 3–5), = 1.0 mm (Figs. 6–9). Abbreviations: ant = antenna; cyb = cylindrical brushes; lbr = labrum.

and Kovac (1994). The specimens upon which this study is based are in the Coleção Entomológica Costa Lima (CECL), Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro (UFRRJ), Seropédica, Rio de Janeiro, RJ, Brasil.

Chalcidomorphina aurata Enderlein, 1914
(Figs. 1–9)

Chalcidomorphina aurata: Enderlein 1914 (original description); Lindner 1951 (suppl. descr., figs.); James 1973 (catalogue); James 1974 (revision, figs.); James, McFadden, and Woodley 1980 (suppl. descr., key to females, notes on the males, figs.).

Distribution.—Neotropical: Mexico, Panama, Colombia, Peru, Brazil.

Larva (and puparium).—Length 5.0 to 5.3 mm, flattened dorsoventrally, lateral margins of body segments strongly arched. Cuticle with usual mosaic appearance, some cells forming characteristic patches and plaques on abdominal segments 6 and 8. Chromatic pattern yellowish brown, with some dark punctuations (Fig. 2).

Head: Subconical, moderately flat; mandibular-maxillary complex with well developed, cylindrical brushes almost as long as labrum, in dorsal view (Fig. 3); labrum triangular. Antenna short, rising at anterior part of head. Eyes prominent, rounded, arising at the posterior part of the head. Two pairs of lateral setae, one pair of clypeofrontal setae and one pair of dorsolateral setae inserted above eyes; three pairs of ventrolateral setae and three pairs of spine-like ventral setae (Figs. 3–4).

Thorax: First segment shorter than others. Spiracle prominent and V-shaped, with a small anterolateral spiracular seta, in lateral view with two dorsal setae and one ventral seta (Fig. 5). First segment with two rows of setae in dorsal view: two pairs of anterodorsal setae and three pairs of dorsal setae. In ventral view, two pairs of ventral setae and one pair of ventrolateral setae near spiracle. Second and third segments with one row of setae with four pairs of dorsal setae and three pairs of ventral setae (Fig. 2).

Abdomen: Segments 1–7 similar in shape to thoracic segments (Fig. 2), with a row of five pairs of dorsal setae and four pair of ventral setae (Fig. 6–7); ventromedial line of segment 6 with an elliptical sternal patch (Fig. 7); segment 8 rounded, with three pairs of conspicuous plaques along dorsomedial line between a pair of pennate dorsocentral setae (Fig. 8), four pairs of lateral setae, apical pair shorter than others; opening of spiracular chamber with a fringe of small setae, anal slit on ventral side emarginate with a long fringe of setae on each side (Fig. 9).

Material examined.—Brazil, Rio de Janeiro, Ilha da Marambaia, 17.II.1998 (R. Xerez col.), 4 females (emerged: 04.III.1998; 2.IV.1998 and 9.IV.1998) and 2 larvae (last instar).

Comments.—*Chalcidomorphina* larvae share some features with the genera keyed by James (1981). The larva keys to the second half of couplet 21. Then, the features are distributed in several couplets. Couplet 21 segregates two groups: first half: [*Berkshiria* + *Neopachygaster*] and second half: [*Gowdeyana* + *Eidalimus* + *Pachygaster* + *Zabrachia*]. However, *Chalcidomorphina* also shares a feature with *Neopachygaster* (second half of couplet 22, three pairs of conspicuous plaques along dorsomedial line of abdominal segment 8) and differs in the same couplet by the shape of sternal patch of abdominal segment 6 (oval in *Neopachygaster*).

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DESCRIPTION OF THE IMMATURE STAGES OF THREE SPECIES OF *EULEPIDOTIS* GUENÉE (LEPIDOPTERA: NOCTUIDAE) WITH NOTES ON THEIR NATURAL HISTORY

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Abstract.—Larvae and pupae of the genus *Eulepidotis* Hübner are described for the first time. The species are *E. merricki* (Holland), *E. juncida* (Guenée), and *E. superior* (Guenée), all of Neotropical distribution. The larval host of *E. merricki* is Spanish-lime, *Melicoccus bijugatus* Jacq. (Sapindaceae), which is cultivated as an ornamental and fruit tree throughout the Caribbean. Larvae of *E. juncida* were reared from *Inga fagifolia* (L.) Willd. ex Benth. (= *Inga laurina* (Sw.) Willd.) (Mimosaceae). Larvae of *E. superior* were defoliating *Quararibea asterolepis* Pitt. (Bombacaceae).

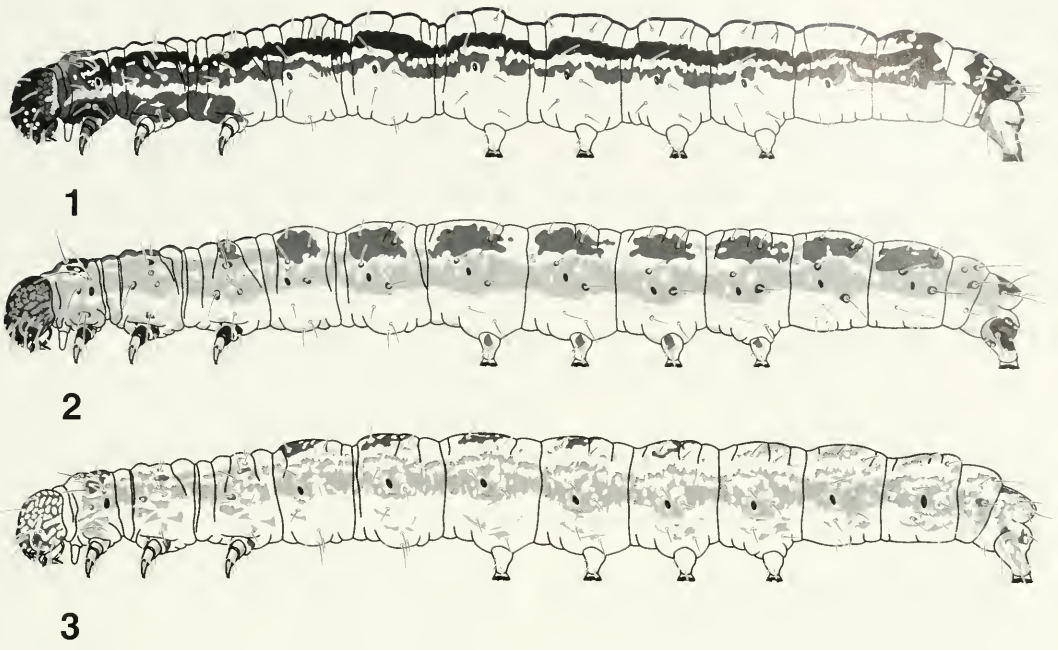
Key Words: *Melicoccus,* Sapindaceae, *Inga,* Mimosaceae, *Quararibea,* Bombacaceae, host plants, Neotropical, Panama, Puerto Rico

Larvae of tropical Lepidoptera are poorly known, and unless reared to adults, they are virtually impossible to identify specifically. We describe for the first time the immature stages of *Eulepidotis* Hübner, a large genus belonging to the subfamily Catocalinae, that is mainly of Neotropical affinity and which comprises 105 species, 3 of which occur in North America (Poole 1989, Poole and Gentili 1996). The immature stages of *E. merricki* (Holland), *E. juncida* (Guenée), and *E. superior* (Guenée) were studied.

There have been two reports of *Eulepidotis* larvae defoliating tropical trees. Wong et al. (1990) reported larvae of *E. superior* defoliating *Quararibea asterolepis* Pitt. (Bombacaceae) on Barro Colorado Island, Panama. Nascimento and Proctor (1994) reported that larvae of *E. phrygionia* Hampson were defoliating a monodominant rainforest of *Peltogyne gracilipes* Ducke (Caesalpiniaceae) on Maracá Island, Roraima, Brazil. Unfortunately no larvae from the latter study were preserved.

Larvae, pupae, and adults of *E. merricki* were sent to one of us (MGP) by Lionel-Pagan, U.S.D.A., Animal and Plant Health Inspection Service, Plant Protection and Quarantine, San Juan, Puerto Rico, for identification. The larvae were defoliating Spanish-lime, *Melicoccus bijugatus* Jacq. (Sapindaceae), a tree used for fruit and as ornamental purposes in the Caribbean. Spanish-lime is native to continental tropical America from Nicaragua to Surinam and is planted widely and becoming naturalized in the Caribbean (Adams 1972, Proctor 1984).

One of us (AA) reared the immature stages of *E. juncida* and *E. superior.* The host of *E. juncida* was *Inga fagifolia* (L.) Willd. ex Benth. (= *Ingalaurina* (Sw.)



Figs. 1–3. Larval habitus. 1, *Eulepidotis merricki*. 2, *E. juncida*. 3, *E. superior*.

Willd.) (Mimosaceae). The host of *Eulepidotis superior* is *Quararibea asterolepis* Pitt (Bombacaceae).

Methods and Materials

Twenty-two larvae of *E. juncida* were collected and designated as Aiello Lot 80-003. Fifteen of the larvae were preserved in 80% ethanol. Seven were placed in a cylindrical rearing cage along with both old and young foliage. The cage was constructed from petri dishes and aluminum window screen with a circle of paper towel on the floor and measured 10 cm tall by 9 cm in diameter. To maintain and regulate humidity, a damp, folded strip of paper towel was placed on the cage cover, and the entire assembly was kept inside a clear plastic ZipLoc® bag. After pupation the pupae were placed into separately numbered cages to await eclosion. Fifteen larvae, one pupa, and four adults with associated pupal skins are in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Three larvae and 10 pupae of *E. superior* were obtained and designated as Aiello Lot 85-19. The larvae were preserved in 80% ethanol, and seven adults with associated pupal skins were reared and are in the collection of the Smithsonian Tropical Research Institute, Republic of Panama.

Key to Known *Eulepidotis* Larvae

1. Head dark brown to black, reticulate pattern reduced; mid-dorsal stripe black, solid (Fig. 1); setae A1—A2—A3 form an acute angle (Fig. 5) . . . . . *E. merricki* (Holland)
– Head brown, reticulate pattern covers most of head; mid-dorsal stripe broken (Figs. 2–3); setae A1—A2—A3 form an obtuse angle (Figs. 12–19) 2
2. Head with reticulate pattern restricted to lateral area; dorsolateral markings on abdomen in pairs (Fig. 2); labrum with one pair of setae on lateral margin (Fig. 14) . . . . *E. juncida* (Guenée)
– Head uniformly covered with a reticulate pattern; abdominal segments with single large dorsal markings (Fig. 3); labrum with two pairs of setae on lateral margin (Fig. 21) . . . . . *E. superior* (Guenée)

KEY TO KNOWN *EULEPIDOTIS* PUPAE

1. Length less than 12 mm; labial palpus disjunct (Fig. 30) ..... *E. juncida* (Guenée)
– Length greater than 13 mm; labial palpus continuous (Figs. 25 and 34) 2
2. Profemur absent (Fig. 25) ..... *E. merricki* (Holland)
– Profemur present (Fig. 34) ..... *E. superior* (Guenée)

Eulepidotis merricki (Holland) (Figs. 1, 4–10, 25–29)

Larva

Diagnosis.—Dorsal black stripe from pronotum to transverse stripe on segment 8 and extending beyond band to segment 9. Head black to dark brown, without reticulate pattern.

Description.—*Head* (Figs. 5–10): Width of head capsule 1.8 ± .06 mm (range, 1.8–1.9 mm) (n = 5). Black to dark brown; ecdysial line, epicranial suture, and posterior margin of head to stemmatal area cream. Prothoracic shield dark brown; medial patch dark brown withthin cream stripe; dorsolateral band cream; lateral edges dark brown. Labrum medially cleft; 3 pairs of dorsal setae forming an oblique line medially (Fig. 7); 3 pairs of ventral epipharyngeal setae (Fig. 8). Mandible with 3 distinct broad teeth; oral surface with broad molar-bearing process (Fig. 10).

Thorax: Dorsal stripe black; dorsolateral band cream; lateral band broad, black, divided by a series of cream spots, extending to just below setae L1 and L3. Legs dark brown. Underside dark brown to metathoracic legs, caudal half of mesothorax cream; V1 setae surrounded by dark brown spot.

Abdomen (Fig. 1): Dorsal stripe black to broad transverse band on segment 8 and extends between segments 8 and 9; dorsolateral band cream; lateral stripe black; lower lateral stripe with irregular margins, cream; spiracular stripe black with irregular margins and not enclosing spiracle; below spiracles and venter cream. Prolegs cream; plantae black; crochets in an uniordinal mesoseries. Segments 1 and 2 with 3 SV setae.

Pupa

Diagnosis.—Labial palpi present, continuous; profemur absent.

Description.— *Male* (Figs. 25–27)*:* Length 15.8 ± 1.04 mm (range, 15.0–17.0 mm) (n = 3). Labial palpi present, continuous. Profemur absent. Mesothoracic leg-reaching eye. Wings do not extend beyond caudal margin of segment 4. Segments 1–3 and 8 with shallow circular pits on dorsum; segments 4–7 with shallow circular pits in a dense band extending about ¼ width of segment caudally and completely encircling segments 5–7; segment 9 smooth. Genital opening on a circular plate. Anal opening below genital opening. Cremaster consisting of a large median pair of slightly curved hooks and 3 pairs of small hooks, 1 pair located mediodorsally, 2 pairs located laterally (Fig. 27).

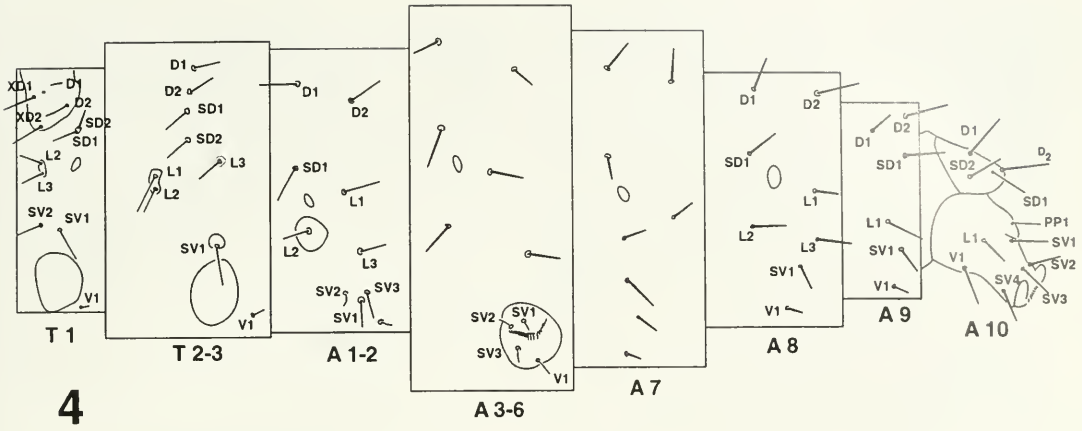
Female (Figs. 28–29): Similar to male except: length 15.2 ± 0.35 mm (range, 15.0–15.5 mm) (n = 2). Genital opening at caudal border of segment 8, dividing segment 8 ventrally. Anal opening well caudad of genital opening.

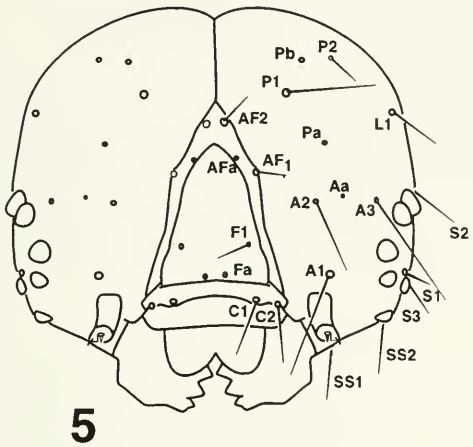
Host.—*Melicoccus bijugatus* Jacq.; Family Sapindaceae; common names: Spanish-lime, genip, honeyberry, mamoncillo, quenette, Quenepa, Hongibeere.

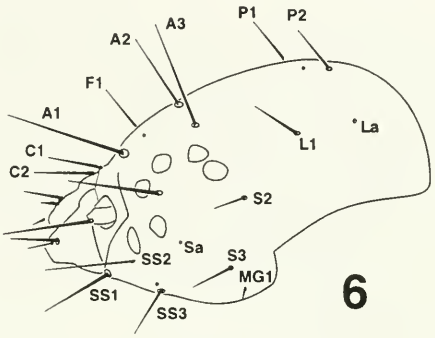
Natural history.—The only information known is that thousands of larvae were defoliating the host plant (Lionel Pagan, personal communication).

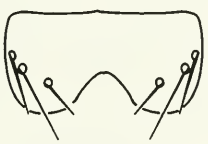
Discussion.—The adult of *E. merricki* most closely resembles *Eulepidotis carcistola* Hampson and *E. fumata* (Felder and Rogenhofer). In *E. merricki* the prothorax and tegula have a black stripe; this is absent in *E. carcistola* and *E. fumata.* An elongate white spot at the base of median line of the forewing is larger and more distinct in *E. carcistola* than in *E. merricki* and *E. fumata.* The forewing lines in *E. fumata* are very faint compared with the bold distinct lines in *E. merricki.*

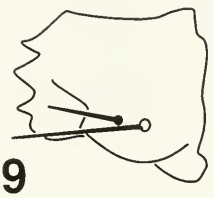
Eulepidotis merricki was described from a specimen collected flying around low



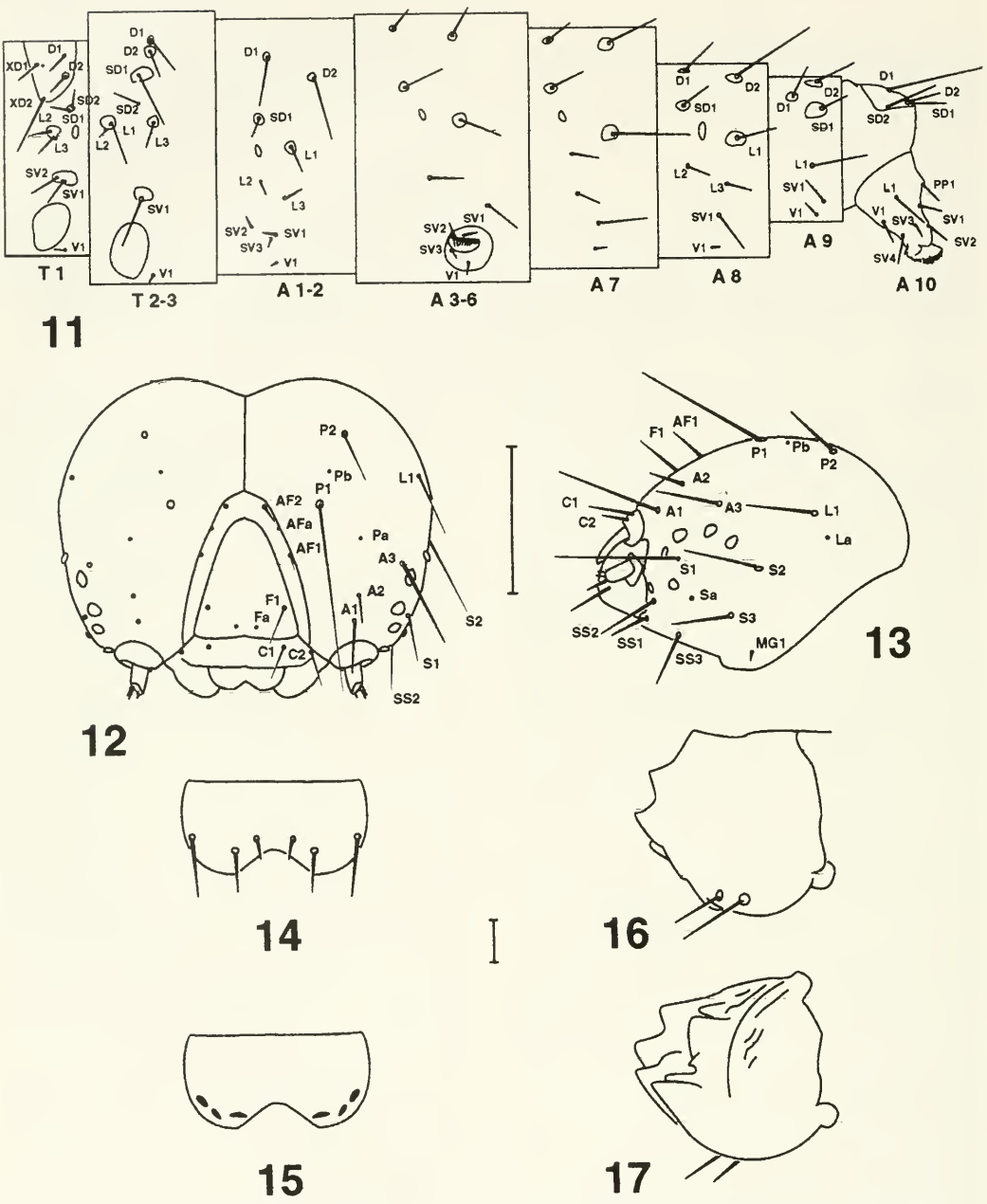








Figs. 4–10. *Eulepidotis merricki* larva. 4, Setal map. 5, Head. 6, Head, lateral view (scale = 0.5 mm). 7, Labrum, dorsal view. 8, Labrum, ventral view. 9, Mandible, dorsal view. 10, Mandible, ventral view (scale = 0.1 mm).



Figs. 11–17. *Eulepidotis juncida* larva. 11, Setal map. 12, Head. 13, Head, lateral view (scale = 0.5 mm). 14, Labrum, dorsal view. 15, Labrum, ventral view. 16, Mandible, dorsal view. 17, Mandible, ventral view (scale = 0.1 mm).

herbage outside New Brighton, Pennsylvania, on August 5, 1900. Holland (1902) in the original description stated that it is very close to *Palindia mabis* Guenée (= *E. juncida* (Guenée)) which he confused as a synonym of *Palindia fumata* Felder and Rogenhofer (= *E. fumata).* The point is that *E. merricki* is not a Nearctic species but a Neotropical one, and that H. D. Merrick just happened to collect a specimen that

was somehow imported from the Neotropics, possibly on tropical fruits. There are no other specimens of *E. merricki* from the Nearctic in the National Museum, Washington, D.C., or The Natural History Museum, London, collections. In Franclemont and Todd (1983) *E. merricki* is noted as being of questionable occurrence in America north of Mexico.

Eulepidotis merricki has a Caribbean distribution, having been collected from Jamaica, Cuba, and Puerto Rico.

Eulepidotis juncida (Guenée)
(Figs. 2, 11–17, 30–33)

Larva

Diagnosis.—Head brown with reticulate pattern restricted to lateral area. Dorsum of abdomen with pair of dorsolateral brown patches encompassing setae D1 and D2.

Description.—*Head* (Figs. 12–17): Width of head capsule for three instars as follows: 1.2 mm (n = 1); 1.8 ± .03 mm (range, 1.7–1.8 mm) (n = 7); 2.0 ± .05 mm (range, 2.0–2.1 mm) (n = 7). Brown with lateral reticulate pattern; adfrontal area from ecdysial line to just beyond setae AF1 cream; setae P1 and P2 with cream pinacula. Labrum medially cleft; 3 pairs of dorsal setae with second pair below other pairs; 3 pairs of ventral epipharyngeal setae (Fig. 15). Mandible with 2 distinct broad teeth, 1 smaller tooth mostly obscured from dorsal view; oral surface with a broad molar-bearing process with small pointed processes on either side (Fig. 17).

Thorax: Prothoracic shield brown; dorsolateral band cream; small cream patch between D2 and XD2. Dorsal stripe or patch on segment 2 brown, on segment 3 cream; dorsolateral band cream; lateral band broad, brown, interrupted by several cream spots, extending to just below setae L1 and L3. Legs brown. Underside mostly cream, brown shading between coxae and encompassing V1 setae.

Abdomen (Fig. 2): Dorsum with pair of dorsolateral brown patches encompassing setae D1 and D2; lower lateral stripe cream, consisting of irregular spots and stripes that are more or less contiguous to segment 6, line not contiguous to absent on segments 7 to 9; spiracular band brown, broad, extending below L1 seta; below L1 seta and venter cream. Prolegs cream to brown laterally; plantae cream; crochets in an uniordinal mesoseries. Segments 1 and 2 with 3 SV setae.

Pupa

Diagnosis.—Small, less than 12 mm long. Labial palpi present, but disjunct. Profemur present.

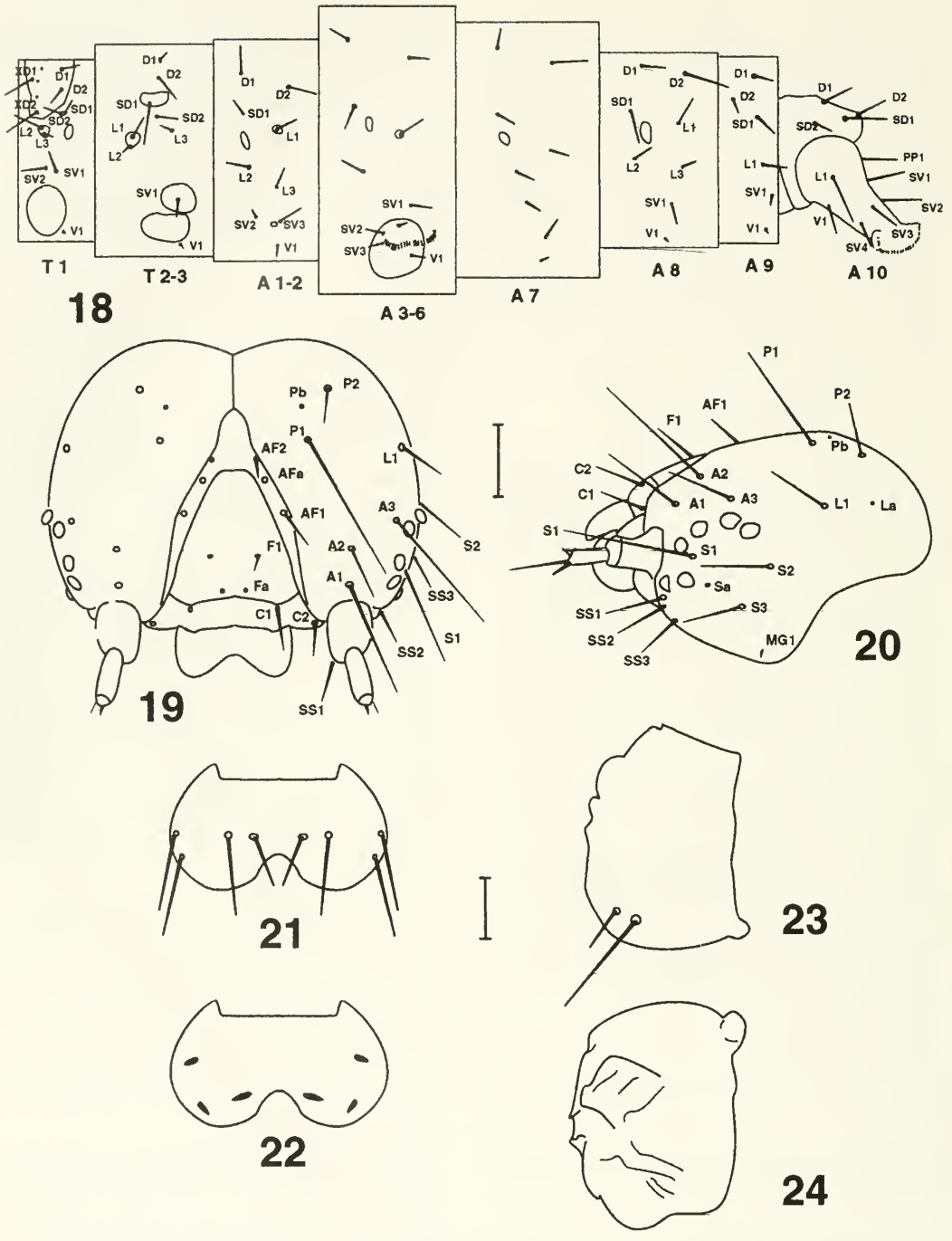
Description.—*Male* (Figs. 30–33): Length 9.3 ± 0.40 (range, 8.9–9.7 mm) (n = 3). Labial palpi present, disjunct. Profemur present. Mesothoracic leg reaching eye. Wings do not extend beyond caudal margin of segment 4. Segments 1–3 and 8 dorsum with shallow circular pits; segments 4–7 with shallow circular pits in a dense band extending about ¼ width of segment caudally and completely encircling segments 5–7; segment 9 smooth. Genital opening on a circular plate. Anal opening caudad of genital opening. Cremaster consisting of a large median pair of curved hooks and 3 pairs of small hooks, 1 pair located mediodorsally, 2 pairs located laterally (Figs. 32–33).

Female (Fig. 33): Similar to male except: length 9.4 ± 0.99 mm (range, 15.0–17.0 mm) (n = 2). Genital opening at caudal border of segment 8, dividing segment 8 ventrally. Anal opening well caudad of genital opening.

Host.—*Inga fagifolia* (L.) Willd. ex Benth. (= *Inga laurina* (Sw.) Willd.); family Mimosaceae.

Natural history.—On March 5, 1980, an outbreak of larvae occurred on Barro Colorado Island, Republic of Panama, near the 900 meter mark on Thomas Barbour Trail on the central plateau of the island. Larvae were so abundant that the rainlike sound of their fecula landing on the leaf litter could be heard many meters away.

Although the majority were in the cano-



Figs. 18–24. *Eulepidotis superior* larva. 18, Setal map. 19, Head. 20, Head, lateral view (scale = 0.5 mm). 21, Labrum, dorsal view. 22, Labrum, ventral view. 23, Mandible, dorsal view. 24, Mandible, ventral view (scale = 0.1 mm).

py, larvae fed at various levels in the tree eating only young leaves. They dropped on silk lines to the forest floor and surrounding vegetation to molt. Molting took place under a sheet of silk across a leaf. Larvae walked by "looping," as do geometrids, but they have the full complement of five pairs of prolegs.

Some larvae dropped, presumably in response to some perceived danger, and began reascending almost immediately. They progressed slowly by gathering the silk line into a ball using their thoracic legs. Upon completion of their journey, they abandoned the ball of silk.

Seven larvae were brought into the laboratory on March 5; one died on March 7. The remaining six molted on March 9, and late on March 10 began preparing pupation chambers of fecula and intact leaves on the cage floor. Five pupated on March 11, and the sixth larva failed to pupate and died on March 12. Two adults eclosed during the night of March 19–20, and two more eclosed during the night of March 20–21. The fifth pupa died and was preserved. Pupal duration was 9 days for females and 10 days for males.

Discussion.—In the adult stage, *E. juncida* is similar to *E. juliata* (Stoll). In *E. juncida* the median brownish-yellow stripe extends from the costa to the inner margin of forewing, in contrast to *E. juncida,* which has a more whitish-yellow median stripe that does not extend to the inner margin.

Eulepidotis juncida has a wide distribution from Mexico to Panama in Central America and from Guyana, Venezuela, and Colombia to Bolivia in South America. *Eulepidotis juliata* is known, so far, only from Guyana, Venezuela, and Bolivia.

Eulepidotis superior (Guenée)
(Figs. 3, 18–24, 34–37)
Larva

Diagnosis.—Reticulated pattern covering entire head. A single large mid-dorsal light brown (in alcohol specimens) mark on all abdominal segments.

Description.—*Head* (Figs. 19–24): Width of head capsule for two instars as follows: 1.9 mm (n = 1); 2.6 mm (n = 2). Brown with cream reticulated pattern. Labrum cream, medially cleft; 3 pairs of dorsal setae forming a straight line medially; 2 pairs of small setae along lateral edge; 3 pairs of ventral epipharyngeal setae (Fig. 22). Mandible with 2 outer setae; cutting surface with 3 indistinct teeth; oral surface with broad molar-bearing process (Fig. 24).

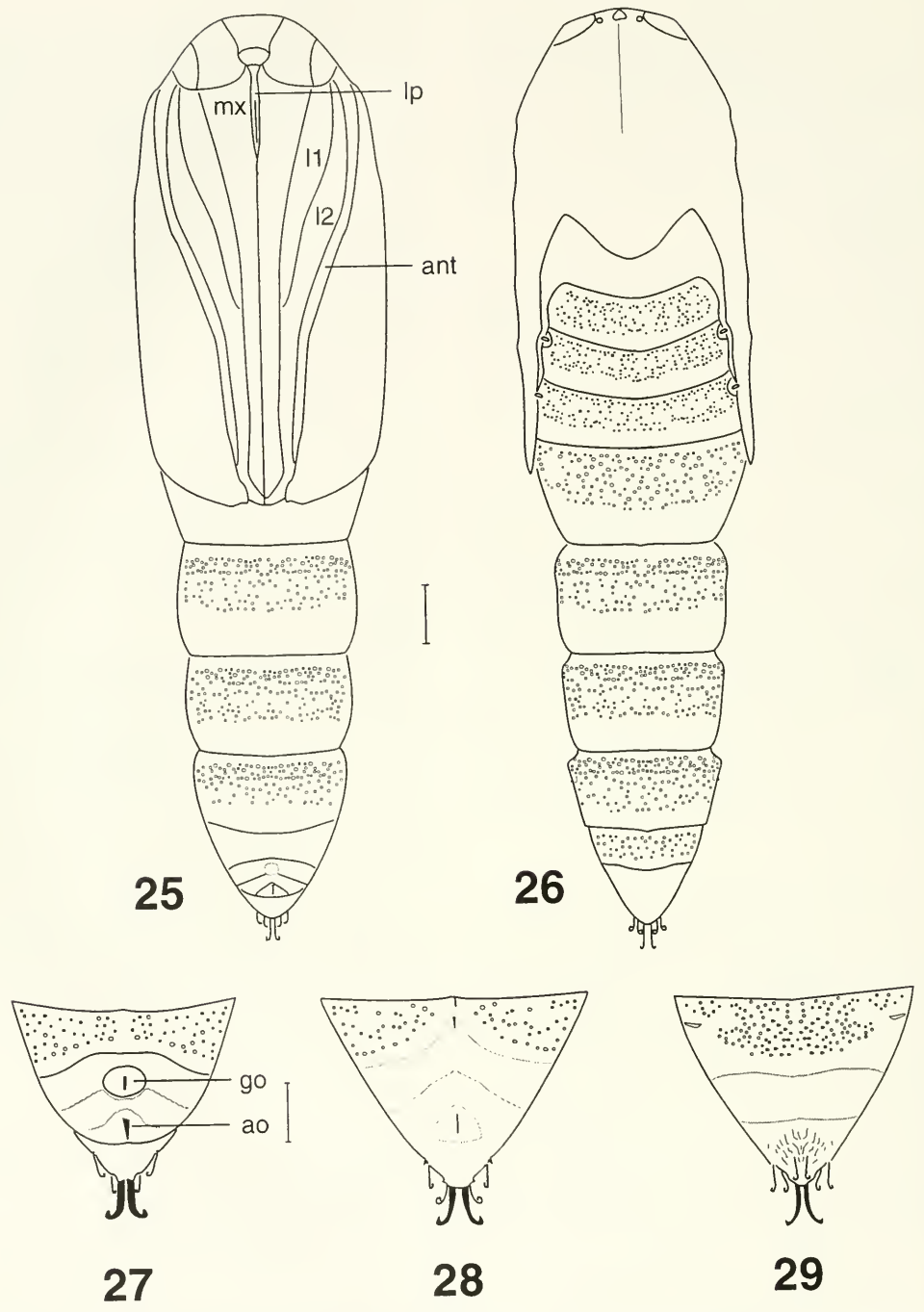
Thorax: Prothoracic shield brown; mid-dorsal stripe faint, cream; lateral stripe wide, cream; marked with various spots and patches of cream. Cream dorsally with a few faint mid-dorsal patches of brown. Prothorax with SD and L setal groups on brown pinacula. Thoracic segments 2 and 3 with seta SD1 and setae L1 and L3 on brown pinacula. Legs cream. Underside cream.

Abdomen (Fig. 3): Mid-dorsal quadrate marks light brown, less distinct on segments 4–6 and 9; dorsolateral band cream; lateral band broad, brown, broken by series of cream spots along dorsal margin; distinct cream spots slightly dorsal and posterior to spiracles. D1 seta inside, D2 seta outside dorsal patch. Segments 1 and 2 with SD1, L1, and L3 on brown pinacula. Segments 3–6 and 8 with SD1 and L group setae on brown pinacula. Prolegs cream; crochets in an uniordinal mesoseries. Segments 1 and 2 with 2 SV setae, SV1 represented by a sclerotized ring near SV3.

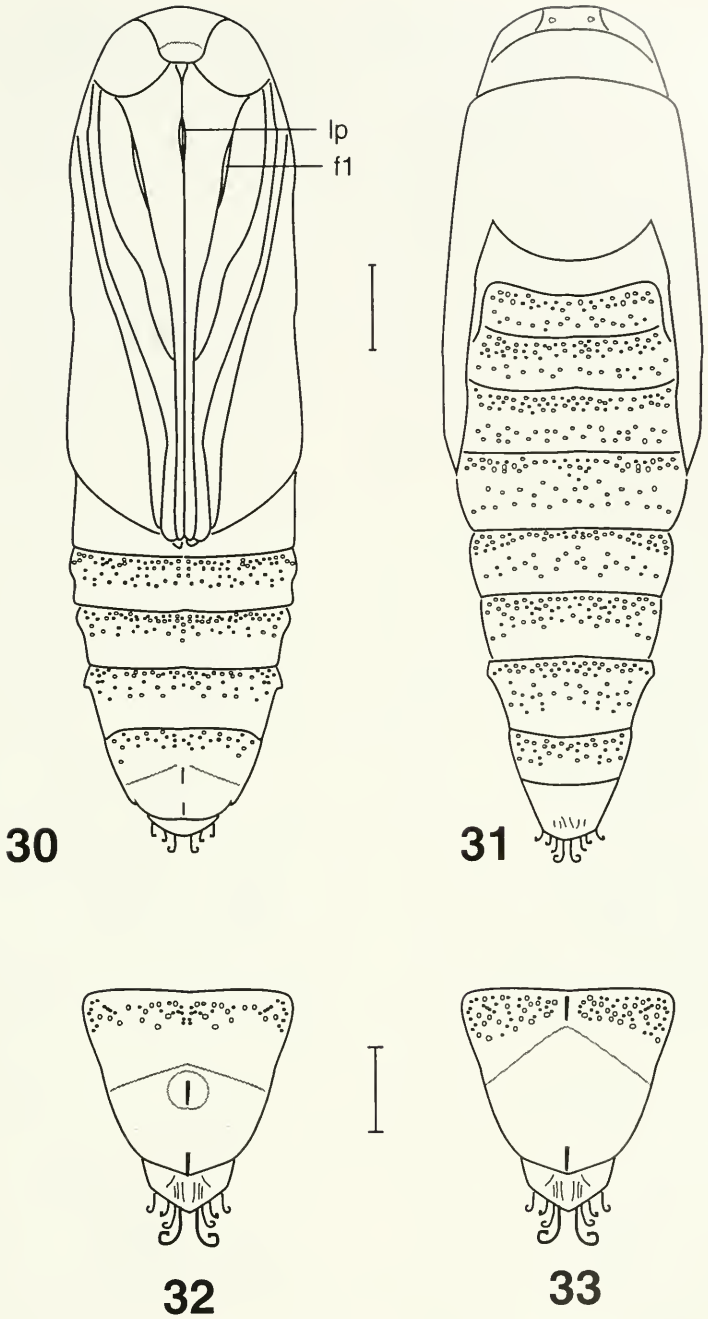
Pupa

Diagnosis.—Labial palpus present, continuous; profemur present.

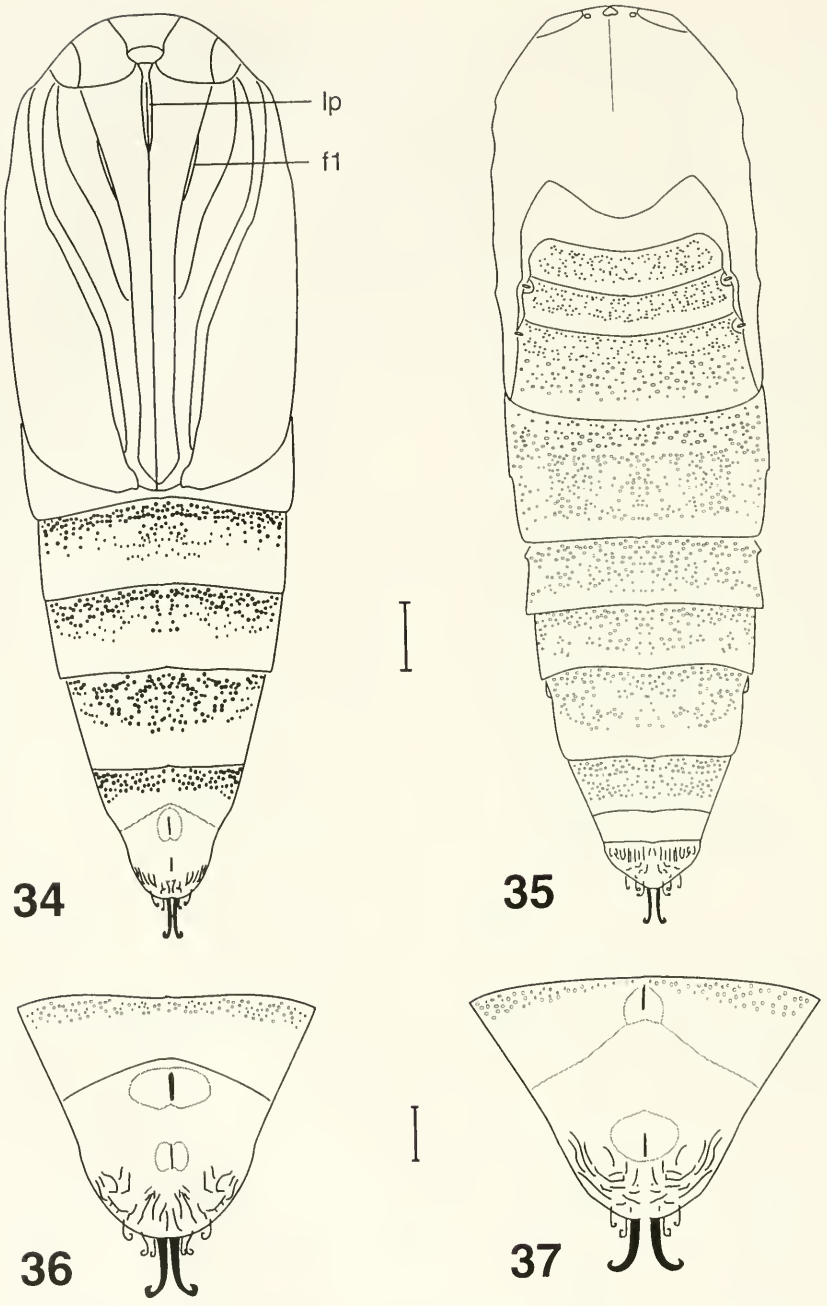
Description.—*Male* (Figs. 34–36): Length 15.8 ± 1.04 mm (range, 15.6–19.6 mm) (n = 4). Labial palpi present, elongate, continuous. Profemur present. Mesothoracic leg reaching eye. Wings do not extend beyond caudal margin of segment 4. Segments 1–3 and 8 with shallow circular pits on dorsum; segments 4–7 with shallow circular pits in a dense band extending about ¼ width of segment caudally and complete-



Figs. 25–29. *Eulepidotis merricki* pupa. 25, ♂ ventral view. 26, ♂ dorsal view (scale = 1.0 mm). 27, ♂ ventral view of terminal segments. 28, ♀ ventral view of terminal segments. 29, Dorsal view of terminal segments (scale = 0.5 mm). Abbreviations: ant =antenna; ao = anal opening; go = genital opening; lp = labial palpi; l1 = prothoracic leg; l2 = mesothoracic leg; mx = maxilla.



Figs. 30–33. *Eulepidotis juncida* pupa. 30, ♂ ventral view. 31, ♂ dorsal view (scale = 1.0 mm). 32, ♂ ventral view of terminal segments. 33, ♀ ventral view of terminal segments (scale = 0.5 mm). Abbreviations: f1 = femur of prothoracic leg; lp = labial palpi.



Figs. 34–37. *Eulepidotis superior* pupa. 34, ♂ ventral view. 35, ♂ dorsal view (scale = 1.0 mm). 36, ♂ ventral view of terminal segments. 37, ♀ ventral view of terminal segments (scale = 0.5 mm). Abbreviations: f1 = femur of prothoracic leg; lp = labial palpi.

ly encircling segments 5–7; segment 9 smooth. Genital opening on an oval plate. Anal opening caudad of genital opening. Cremaster consisting of a large median pair of curved hooks and 3 pairs of small hooks, 1 pair located mediodorsally, 2 pairs located laterally (Fig. 36).

Female (Fig. 37): Similar to male except: length 16.1 ± 1.03 mm (range, 15.0–17.0 mm) (n=3). Genital opening at caudal border of segment 8, dividing segment 8 ventrally. Anal opening well caudad of genital opening.

Host.—*Quararibea asterolepis* Pitt.; family Bombacaceae.

Natural History.—During late May through early June 1985, a massive, highly synchronized outbreak of larvae was observed on the central plateau of Barro Colorado Island, Republic of Panama (Wong et al. 1990). The larval host plant was undergoing leaf flush and the larvae were feeding on young leaves and often defoliating the trees. Once feeding was completed, the larvae descended on silk lines and pupated beneath dried leaves on the forest floor. Larvae were so abundant that it was difficult to avoid walking into their silk lines or stepping on larvae and pupae.

A total of 10 pupae and 3 larvae were brought to one of us (AA) by Maria Wong, Seiji Tanaka, and Peter Becker. Three pupae died, and seven were reared to adults. Adult no. 1 (♀) eclosed 21 June from a pupa collected 7 June. Adult nos. 4 (♂) and 5 (♀) eclosed 23 and 24 June, respectively, from pupae collected 11 June. Adult nos. 6–9 eclosed 18 June (♀), 20 June (♂), and 21 June (2♂♂), respectively, from pupae collected 14 June. All eclosions took place in early evening, some as early as 5:30 PM, and others as late as 9 PM.

Discussion.—Adults of *E. superior* are the largest (forewing length 13–9.5 mm) of the brown species of *Eulepidotis* and cannot be confused with any other species in the genus. It is distributed from Mexico to Panama in Central America, northwestern South Americain Venezuela, Colombia, and Ecuador, and in the Caribbean on the islands of Puerto Rico, Grenada, and St. Lucia.

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OBSERVATIONS ON THE PREY AND NEST CLUSTERS OF *PODALONIA VALIDA* (CRESSON) (HYMENOPTERA: SPHECIDAE)

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Abstract.—In northern Colorado, *Podalonia valida* preyed upon mature larvae of the saltmarsh caterpillar, *Estigmene acrea* (Drury), the same prey it uses in Arizona. Prey were deposited in shallow, single-celled nests that occurred within clusters probably provisioned by single females. Because females forage for abundant nearby prey, stock each nest cell with a single caterpillar, and dig simple nests in a localized area, they have the potential to provision multiple nests over short time periods. Several observations are consistent with this hypothesis. First, within clusters of nest cells, there was a high degree of synchrony in developmental stages of the wasps, suggesting that eggs were laid in quick succession. Second, dissections showed that female *P. valida* carry more mature eggs in their ovaries than is typical for non-parasitoid aculeate wasps.

Key Words: Digger wasp, Sphecidae, nesting behavior, egg size, *Estigmene acrea*, saltmarsh caterpillar, Arctiidae

Wasps of the genus *Podalonia* dig short burrows terminating in a cell provisioned with a single prey (Bohart and Menke 1976). *Podalonia luctuosa* (Smith) (O'Brien and Kurczewski 1982), *Podalonia robusta* (Cresson) (Kurczewski et al. 1992), and *Podalonia argentifrons* (Cresson) (O'Brien 1983) restrict themselves to cutworms (Noctuidae), but may take a variety of species at any one site. Similarly, *Podalonia occidentalis* Murray apparently prey solely on tent caterpillars (Lasiocampidae: *Malacosoma*) (Evans 1987) and *Podalonia valida* (Cresson) limit themselves to arctiid moth caterpillars. Steiner (1974, 1975) found *P. valida* specializing on saltmarsh caterpillars (*Estigmene acrea* (Drury)) in southern Arizona, whereas Rust et al. (1985) found two female *P. valida* taking *Apantesis proxima* (Guérin-Méneville) on San Clemente Island, California. Here, we present results of our observations of the nesting behavior and prey of *P. valida* in northern Colorado and compare our findings to those of Steiner, who concentrated on the hunting and territorial behavior of females.

METHODS

We studied *P. valida* females at the Pawnee National Grasslands in northern Weld Co., Colorado, from 12 July to 13 August 1984. The site was situated along a sandy, little-used road that passed through prairie consisting of grasses mixed with several common forbs, notably white sweetclover (*Melilotus alba* Desr.) and sunflower (*Helianthus* spp.).

RESULTS AND DISCUSSION

Our 64 prey records indicate that *P. valida* preyed exclusively on mature larvae of

the saltmarsh caterpillar *Estigmene acrea* (Drury) (Arctiidae), the same species used by this wasp in Arizona (Steiner 1974). The prey of *P. valida,* which were probably taken on their host plants (white sweetclover), were carried in the mandibles as females walked forward straddling the prey. One female carried a caterpillar at least 10 m before reaching her nest. Prey-carrying females occasionally stopped and cached their prey ~5 cm above the soil surface on small plants, where they were left for several minutes while females searched for their nests.

Unlike other species of *Podalonia, P. valida* dig nests before hunting (Steiner 1974, 1975). Each nest at our site consisted of a short, oblique burrow about 1 cm in diameter, terminating in a single 1 × 3 cm cell situated 3–5 cm beneath the soil surface (N = 7). Typically, when digging the nest, a female backed out 5–10 cm from the burrow entrance and scraped soil backwards with her forelegs, while elevating her abdomen, flicking her wings rapidly, and buzzing loudly. Upon returning to her nest with prey, a female dropped it at the entrance, cleared the burrow, and pulled the prey inside while moving backwards. After several minutes inside the nest, during which time she laid an egg on the prey, the female emerged and permanently closed the burrow by scraping in soil from the edge of the burrow and placing lumps of soil or pebbles in the hole. She then tamped the loose soil with her head (mandibles wide open) or with a lump of soil which was held in the mandibles and which broke up due to the impact. The entire sequence between entering the hole with prey and completing closure typically took about 4 minutes.

These observations are in accord with those of Steiner (1974, 1975), who found that individual females provisioned series of single-celled nests within small patches of bare soil sometimes no more than 60 cm across. Although we did not observe individually marked females over prolonged periods, we also found that cells tended to be clustered. In 2 of our 7 excavations of recently completed nests, we unearthed just a single cell, but in the others, we found clusters of 8, 15, 16, 18, and 27 cells within areas no more than 0.25 m^2. Some cells were separated by as little as 5 cm, but were definitely parts of different nests. Clusters of nest cells were well-separated from one another and each was apparently used exclusively by a single female, who vigorously attacking conspecific females intruding upon their nest cluster in interactions that included bouts of grappling between the combatants. Similar interactions between *P. valida* females have been described in detail by Steiner (1975).

The contents of unparasitized and nonmoldy *P. valida* cells within clusters suggest that, if a single female was responsible for all of the cells, some were provisioned during short time intervals. For example, in the cluster of 15 cells, 5 had prey with wasp eggs, 3 had prey with small wasp larvae, and 1 had a large wasp larva. In the cluster of 7 cells, all had prey with unhatched eggs. Similarly, the cluster of 18 cells included 7 prey with wasp eggs and 7 with small wasp larvae, and the cluster of 16 cells contained 7 with eggs or small larvae.

The potential ability of *P. valida* females to provision multiple nests in rapid succession may be possible because they 1) forage for abundant prey nearby, 2) stock each cell with a single prey, and 3) dig simple, shallow nests without searching widely for successive nesting sites. This strategy may allow them to exploit a single developmental stage of a single prey species that is available for just a brief period during the summer. However, the rapid stocking of multiple nests would also require that a female produce the requisite numbers of eggs. Typically, female sphecids carry no more than two mature eggs at a time, although they have three ovarioles in each ovary (Iwata 1964, O'Neill 1985). Nevertheless, the three *P. valida* females that we captured within minutes of their laying eggs had 3, 5, and 6 mature

(or nearly mature) oocytes still in their ovaries. Thus, the latter female had been carrying seven well-developed oocytes just prior to capture and had one ovariole with two mature oocytes. In Iwata's extensive survey of the ovaries of solitary aculeate wasps, only parasitoid sphecids of the genera *Larra* (with up to 21 mature oocytes) and *Chlorion* (with up to 10) carried more mature eggs than the maximum for *P. valida*. Such high levels of short-term fecundity (for a digger wasp), however, may be achieved at the cost of producing smaller eggs. The mature oocytes of *P. valida* ranged in length from 2.6–3.1 mm in length and one egg found on prey was 2.9 mm long. In contrast, in the similarly-sized but less fecund wasp *Philanthus bicinctus* (Mickel), mature oocytes and newly laid eggs ranged as high as 5.4 mm in length, and had perhaps 3–4 times the volume of *P. valida* eggs (O'Neill 1985). *Bembecinus quinquespinosus* (Say) and *Philanthus pulcher* Dalla Torre carry 1–2 mature oocytes within the same size range as *P. valida*, although they are both much smaller wasps.

Of the 86 cells we excavated, four had fly puparia 0.5–1.0 cm below the cell, which in each case-contained the remains of a single saltmarsh caterpillar. One puparium gave rise to a tachinid of the genus *Exorista*, at least one species of which is a known parasitoid of *E. acrea* (Arnaud 1978). The wasps had probably captured previously parasitized caterpillars and suffered incidental cleptoparasitism. Another 23% of the cells contained molded or rotting caterpillars.

Our observations complement those of Steiner (1974, 1975), indicating that two widely separated populations of *P. valida* have identical prey preferences and similar nesting behaviors that are unique for this genus. *Podalonia valida* seems to have adopted a strategy intermediate between those of the relatively high fecundity parasitoid sphecids (*Larra* and *Chlorion*) and the more typical low fecundity nest provisioning species that spend considerable time and energy on each offspring. This strategy is facilitated by the greater number of mature eggs they carry and, perhaps, by shorter periods of searching for potential nest sites once nesting has begun.

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IDENTIFICATION OF LATE-INSTAR NYMPHS OF COCKROACHES (BLATTODEA)

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Abstract.—A dichotomous key to late-instar nymphs of 12 cockroach species common in the United States is presented. Notes on biology, distribution, and taxonomy are given.

Key Words: Insecta, Blattodea, late-instar nymphs, descriptions, dichotomous key

More than 3600 species of cockroaches are known worldwide, 69 of which are found in North America. Fifteen to twenty of these species are of economic importance as nuisance pests. Classification of cockroaches has undergone many changes. Rehn (1951) classified adult cockroaches based on wing characteristics. Princis (1960) provided a comprehensive history of cockroach taxonomy and reported previously unknown information on cockroach evolution. McKittrick (1964) grouped the cockroaches with mantids based on evolutionary studies, morphology of genitalia and proventriculus, and oviposition behavior. Cornwell (1968) provided a thorough review of the history of cockroach classification. He took the reader from 1758 when all cockroaches were placed in the genus *Blatta,* in the order Coleoptera, through the revision of Imms' *Textbook of Entomology* (Richards and Davies 1957) in which cockroaches are placed in their own order, Dictyoptera. Cockroaches are currently placed in the order Blattodea as recognized by the Entomological Society of America (Bosik 1997).

Dichotomous keys to the cockroaches are primarily restricted to the adult stage (Blatchley 1920, Rehn 1950, Pratt and Stojanovich 1962, Dakin and Hays 1970) except for those by Powell and Robinson (1980), Fisk (1987), and Gordon (1992). Powell and Robinson (1980) included only first-instar nymphs of five *Periplaneta* species and Gordon (1992) distinguished the mid-instar nymphs of *Periplaneta americana* and *P. fuliginosa.* Fisk (1987) included nymphs of 16 cockroach species with identification based on comparative characters.

Because behavior and habitat preference differ substantially among species, and development of effective control strategies depends on correct identification, a dichotomous key to late-instar cockroach nymphs is needed. The present work provides a means of identifying 12 of the pest species found in North America.

MATERIALS AND METHODS

Based on their pest status, late-instar nymphs of 12 species of cockroaches representing 3 families (Blaberidae, Blattellidae, and Blattidae) are included in this key. A cockroach may go through 5 to 12 molts before reaching the adult stage. The individual specimens were selected for size (approximately the same size as the adult of the same species). Exact instar was not known for each individual. Specimens of the following eight species were obtained

from colonies maintained by the Clemson University Urban Entomology Laboratory: *Blattella germanica* (L.), *Supella longipalpa* (F.), *Periplaneta americana* (L.), *Periplaneta australasiae* (F.), *Periplaneta brunnea* Burmeister, *Periplaneta fuliginosa* (Serville), *Blatta orientalis* (L.), and *Parcoblatta lata* (Brunner). Three species (*Blattella asahinai* Mizukubo, *Panchlora nivea* [L.], and *Eurycotis floridana* [Walker]) were obtained from the USDA-ARS laboratory in Gainesville, Florida. One species, *Blattella vaga* Hebard, was obtained from Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Ten to twenty specimens of each species were examined for morphological differences, using a dissecting microscope (WILD Heerbrugg Switzerland M5-3984).

Three species of cockroaches in this key are wingless as adults. These wingless species, on close examination, have truncated wings (*B. orientalis* (female), *E. floridana*), or wing pads (female *P. lata*). This character may confuse the identification of the adult form with a late-instar nymph of another species. All characters used in this key can be seen when the specimen is viewed dorsally.

Key to Late-Instar Cockroach Nymphs

1. Body tan. Thorax with 2 dark brown to black parallel lines 2
– Body color variable. Thorax without parallel lines 4
2. Abdomen with 2 tan dots on some or all tergites in center of dark longitudinal area. Abdomen with tan markings on lateral edges separated by dark brown markings between tergites (note: All above characters may vary slightly or may not be present). . . . . *Blattella germanica* (Fig. 2)
– Abdomen with markings different from above 3
3. Abdomen with tan, horizontal bar on some or all tergites in center of dark longitudinal area. Body with black, vertical line through center. Cercus dark brown to black on terminal ends. Abdomen with tan markings on lateral edges separated by dark brown markings between tergites (note: All above characters may vary slightly or may not be present) . . . . . *Blattella vaga* (Fig. 3)
– Abdomen with tan, horizontal bar bearing anterior emargination on some or all tergites in center of dark longitudinal area. Body without black, vetical line. Cercus tan with dark brown to black markings on terminal ends. Abdomen with tan markings on lateral edges not separated by dark brown markings between tergites (note: All above characters may vary slightly or may not be present) . . . . . *Blattella asahinai* (Fig. 4)
4. Cercus longer than distance between their bases 5
– Cercus shorter than distance between their bases 10
5. Body variably black and tan. Pronotum with black horizontal bar bearing anterior and posterior median emarginations . . . . . *Periplaneta australasiae* (Fig. 5)
– Body uniform reddish-brown or with black on lateral edges of abdominal tergites or tan with dark brown markings. Pronotum with markings different from above. 6
6. Pronotum dark brown with tan on lateral edges. 2nd and 3rd thoracic sclerites with horizontal dark brown markings. Length less than 15 mm . . . . . *Supella longipalpa* (Fig. 1)
– Pronotum with markings different than above. 2nd and 3rd thoracic sclerites without horizontal dark brown markings. Length greater than 15 mm 7
7. Pronotum dark with little color variation. Male with styli shorter than 10th tergite . . . . . *Periplaneta fuliginosa* (Fig. 6)
– Pronotum with some color variation, darkened areas. Styli variable 8
8. Abdomen black, with lighter areas in center of tergites. 10th tergite truncate . . . . . *Parcoblatta lata* (Fig. 7)
– Abdomen with color pattern different from above. 10th tergite notched 9
9. Male with styli slightly longer than distance between their bases. Cercus with last segment twice as long as wide (Fig. 8a) . . . . . *Periplaneta americana* (Fig. 8)
– Male with styli shorter than distance between their bases. Cercus with last segment less than twice as long as wide (Fig. 9a) . . . . . *Periplaneta brunnea* (Fig. 9)
10. Body black. Cercus longer than 10th tergite . . . . . *Blatta orientalis* (Fig. 10)
– Body light brown or dark red and black. Cercus as long as, or shorter than, 10th tergite 11
11. Body dark red in center, with black laterally. 9th abdominal tergite with posterior corners prolonged backward into sharp points. Thoracic and abdominal lateral margins forming a smooth line in dorsal view. 10th tergite

shorter than cercus . . . . . *Eurycotis floridana* (Fig. 11)

– Body uniformly reddish brown. 9th abdominal tergite without points. Thoracic and abdominal lateral margins not forming a smooth line in dorsal view. 10th tergite longer than cercus . . . . . *Panchlora nivea* (Fig. 12)

Notes on Species

Supella longipalpa (Fig. 1).—The brown-banded cockroach nymph has a broad black stripe on the pronotum and other black markings on the thorax. It is typically less than 15 mm. This species is found throughout the United States in relatively sanitary conditions such as office buildings. It prefers temperatures over 27°C and is often found above floor level. It will infest furniture, and deposit egg cases behind picture frames and appliances.

Blattella germanica, B. asahinai, and B. vaga are similar species. The German, Asian, and field cockroach nymphs are tan with two broad, dark brown to black longitudinal stripes on the thorax. Because these species are so similar to one another, multiple characters must all be used for identification of species. As late-instar nymphs there are differences in body size between these three species. However, these size variations may overlap.

Blattella germanica (Fig. 2).—When body length is compared to the other two *Blattella* species represented in this key, it usually is the median. The German cockroach is perhaps the most economically important of all cockroach pests. It is found throughout the United States in human habitations, and rarely outside.

Blattella vaga (Fig. 3).—The field cockroach nymph is typically smaller and lighter in color than *B. germanica* and *B. asahinai.* It is found in the southwestern United States in irrigated fields and yards.

Blattella asahinai (Fig. 4).—The Asian cockroach nymph is typically 2 to 3 mm longer than *B. germanica.* Most individuals have three small black dots arranged in a triangle, a character not always observed in *B. germanica* or *B. vaga.* Found primarily outdoors in Florida, it occasionally enters structures.

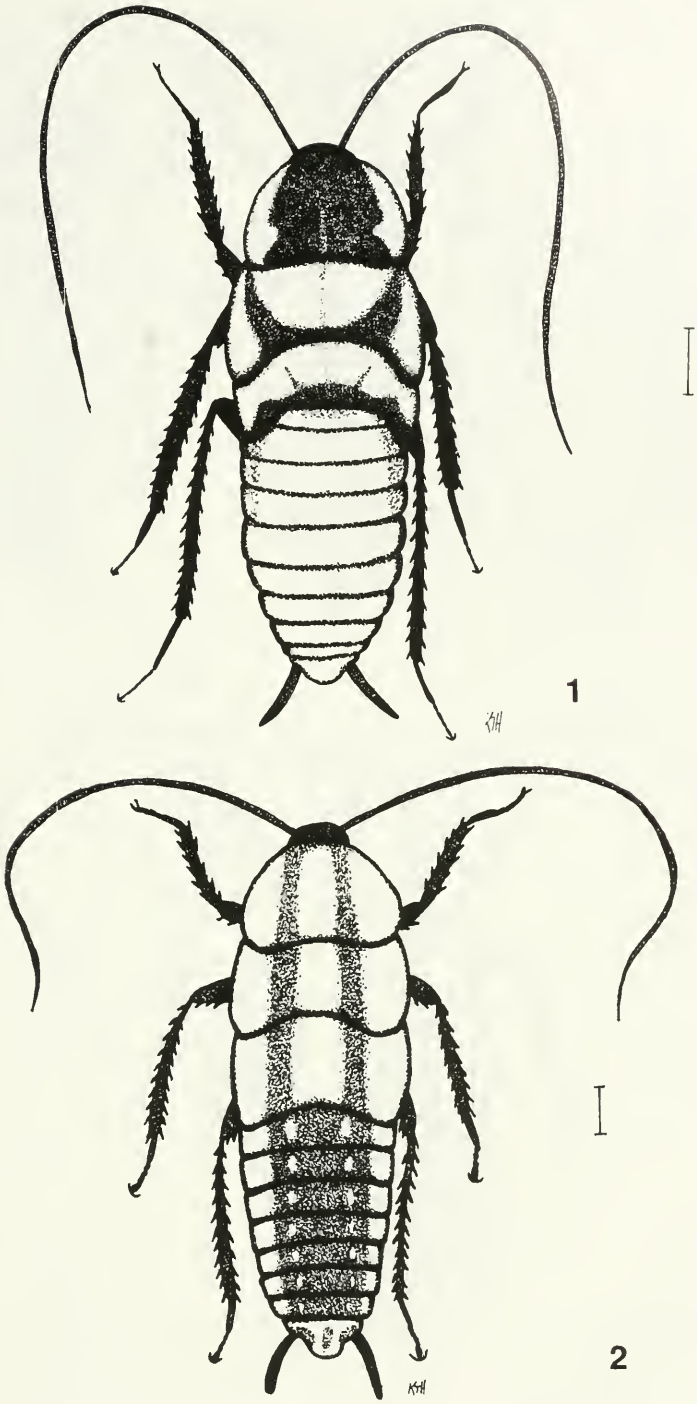
Parcoblatta lata (Fig. 7).—The broad wood cockroach nymph has a uniformly reddish brown thorax. The abdomen is mostly black with lighter markings in the center of the first three to four tergites. The 10th tergite is pointed and unnotched. It is found throughout the United States in wooded habitats. Adult females are wingless. Adult males will occasionally enter buildings.

Periplaneta australasiae (Fig. 5).—The Australian cockroach nymph is easily distinguished by its coloration, it is black and tan and has a dark horizontal bar with anterior and posterior emarginations on the pronotum. The adults share this character. This species is most commonly found in both indoor and outdoor situations in the coastal states of the southern United States and portions of California.

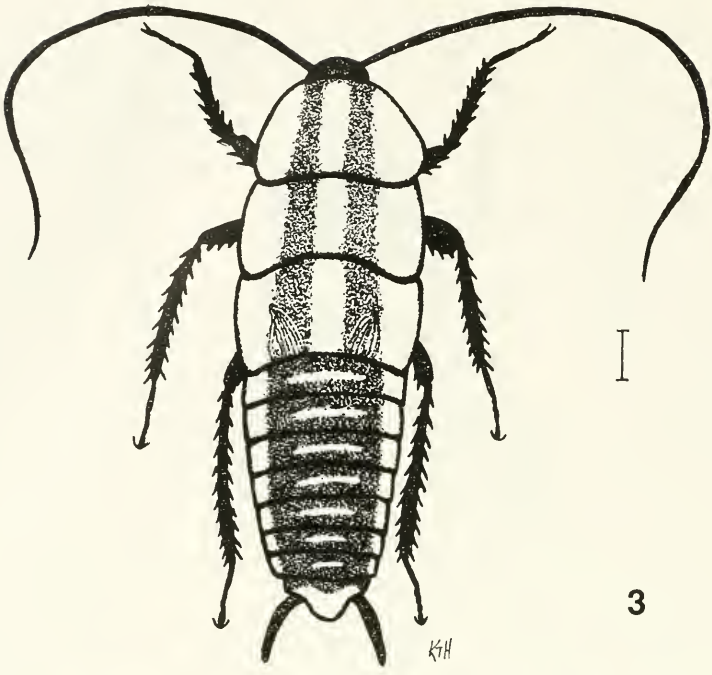
Periplaneta fuliginosa (Fig. 6).—The smokybrown cockroach nymph, very similar to *P. americana* and *P. brunnea,* can be distinguished by its uniform reddish brown color. It is found in the southeastern United States in hot, humid areas in and around structures.

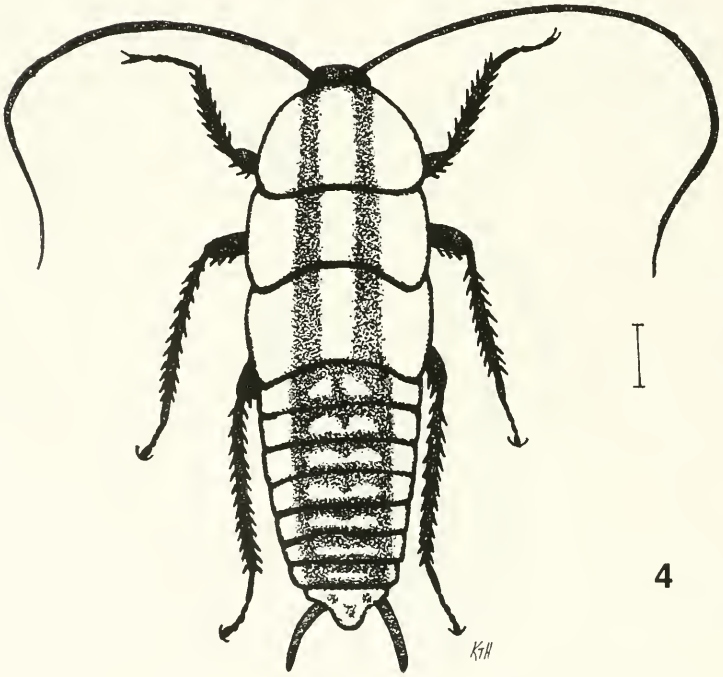
Periplaneta americana (Fig. 8).—Like *P. brunnea,* the American cockroach nymph is reddish brown with variable darkened areas. The cerci are long and slender and the last segment is twice as long as it is wide. If styli are present, they are longer than the distance between their bases. This species is found throughout the United States in association with buildings and warm, humid areas.

Periplaneta brunnea (Fig. 9).—The cerci and styli on the brown cockroach are the key characters used to distinguish this species from *P. americana.* The cerci are more flattened and broader and the last segment is not twice as long as it is wide. If styli are present, they are shorter than the distance between their bases. The brown cockroach is found around buildings in the southeastern United States.

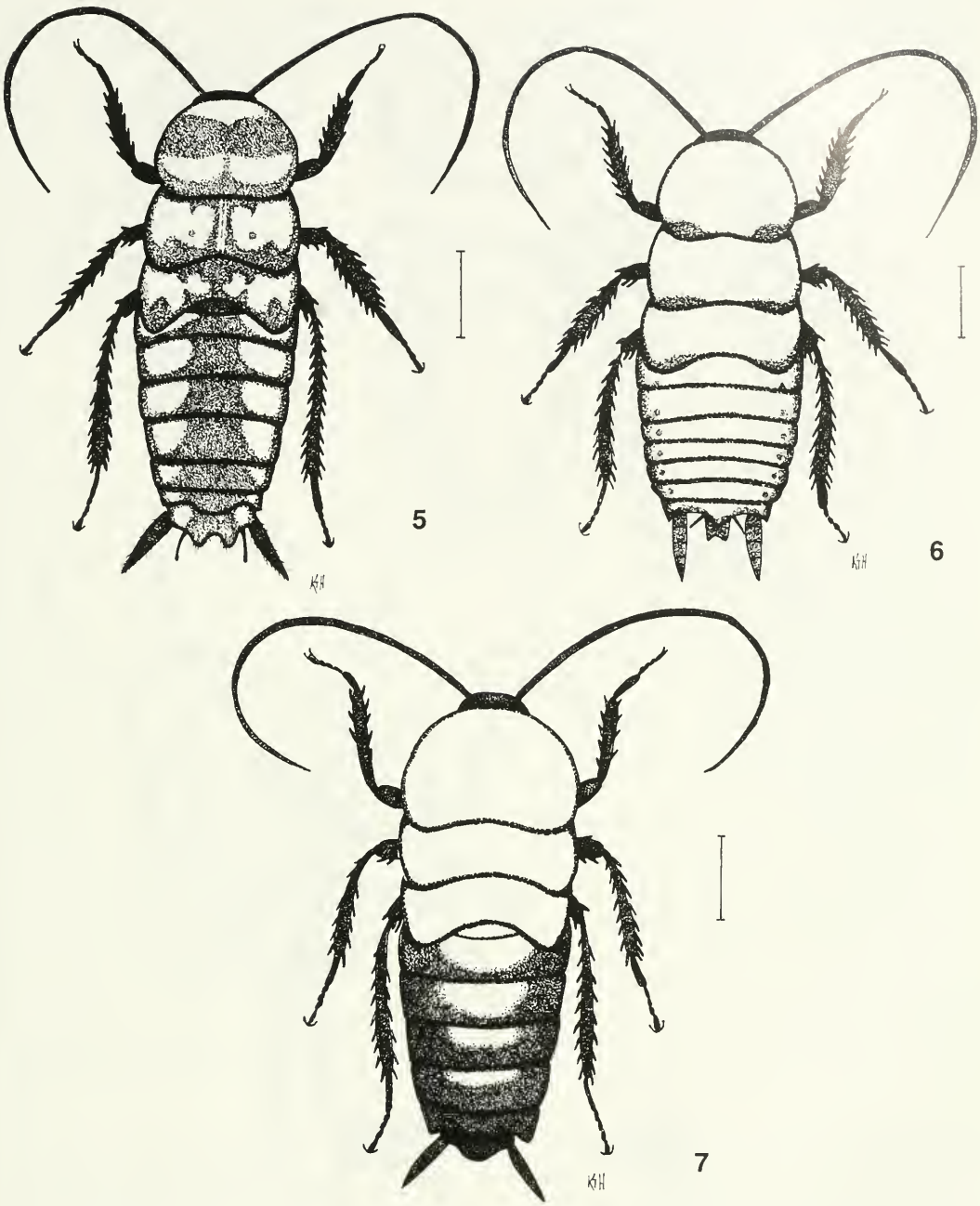


Figs. 1–2. Dorsal view of late-instar nymphs. 1, *Supella longipalpa,* the brown-banded cockroach. 2, *Blatella germanica,* the German cockroach.

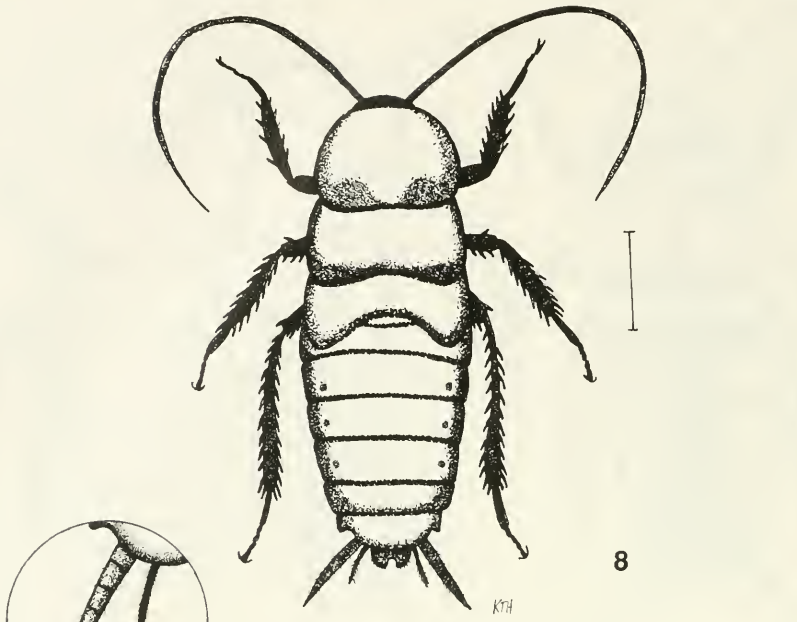


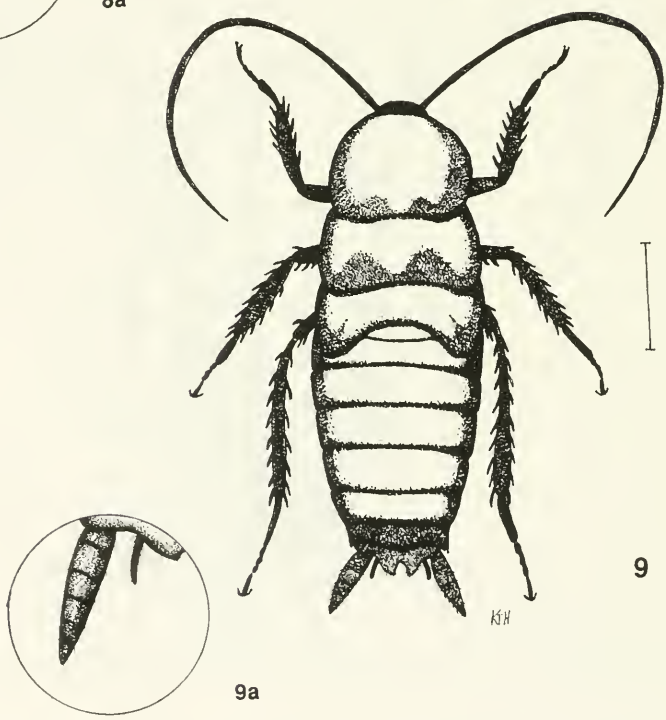


Figs. 3–4. Dorsal view of late-instar nymphs. 3, *Blatella vaga*, field cockroach. 4, *B. asahinai*, the Asian cockroach.

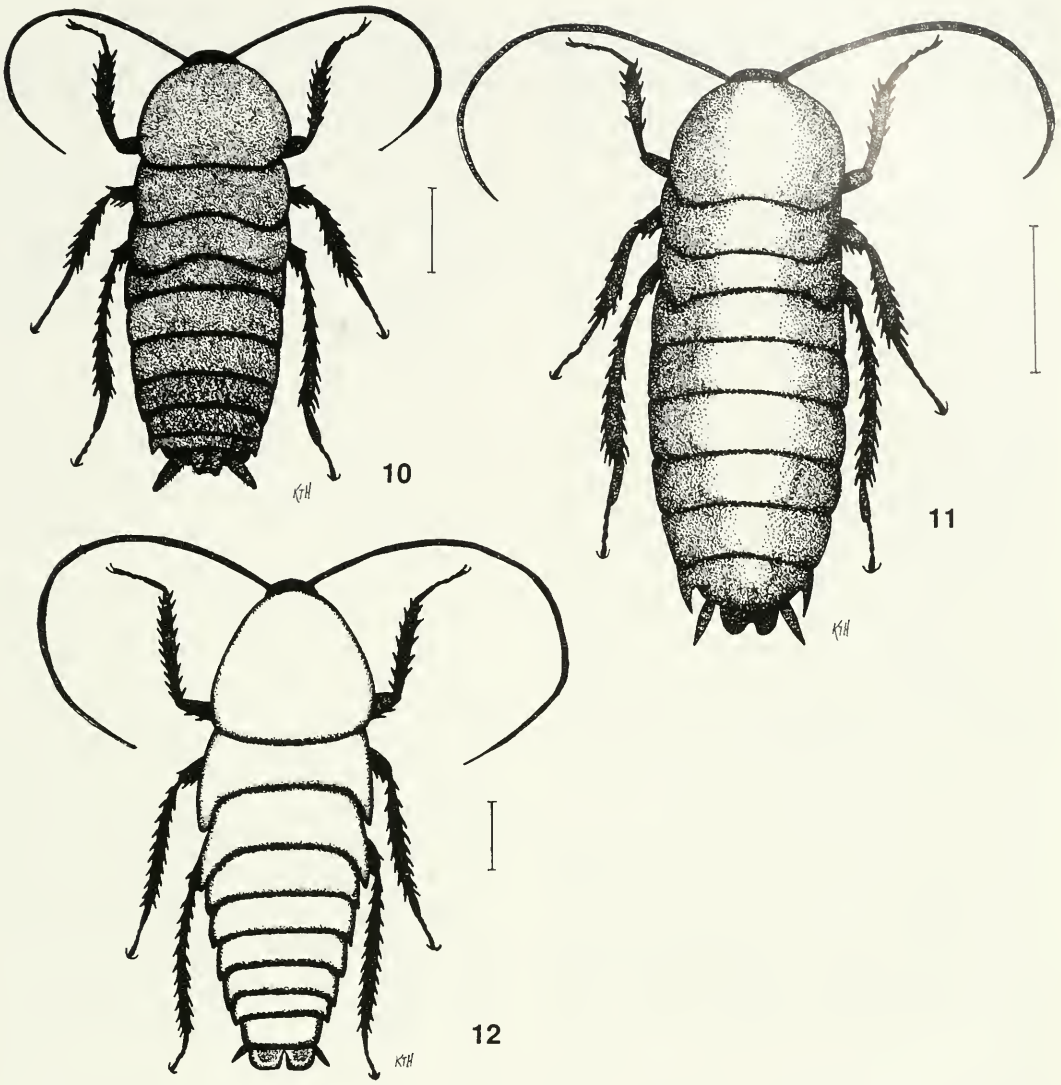


Figs. 5–7. Dorsal view of late-instar nymphs. 5, *Periplaneta australasiae*, the Australian cockroach. 6, *P. fuliginosa*, the smokybrown cockroach. 7, *Parcoblatta lata*, the broad wood cockroach.





Figs. 8–9. Dorsal view of late-instar nymphs. 8, *Periplaneta americana*, the American cockroach; 8a = dorsal view of left cercus. 9, *P. brunnea*, the brown cockroach; 9a = dorsal view of left cercus, note size and shape of last segment.



Figs. 10–12. Dorsal view of late-instar nymphs. 10, *Blatta orientalis,* the Oriental cockroach. 11, *Eurycotis floridana,* the Florida woods cockroach. 12, *Panchlora nivea,* the Cuban cockroach.

Blatta orientalis (Fig. 10).—The Oriental cockroach, easily identified by its uniform dark, reddish-black color, can also have a shiny appearance. Adult females have truncated wings. It is found in and around structures over most of the temperate United States and Canada.

Eurycotis floridana (Fig. 11).—The Florida woods cockroach nymph is comparatively large (35 mm) and dark in color. The center of the body is dark red and the outer edges are black. The posterior corner of the 9th abdominal tergite is prolonged backward to sharp points. Adults have truncated wings. An important pest in Florida, it also is found in southeastern Georgia and along the lower Gulf and Atlantic coasts of the United States. The adult emits an oily liquid with a repellent odor.

Panchlora nivea (Fig. 12).—The Cuban cockroach nymph is reddish brown, and the lateral margins of the thoracic and abdom-

inal segments appear jagged when viewed dorsally. The 10th tergite is rectangular and longer than the cerci. It is found around houses and wooded areas throughout Florida and along the Gulf Coast of the United States.

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STUDIES ON STONEFLIES OF NORTH DAKOTA WITH THE DESCRIPTION OF A NEW *PERLESTA* SPECIES (PLECOPTERA: PERLIDAE)

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Abstract.—Records for fifteen stonefly taxa, including eleven confirmed species are given for North Dakota. Literature records for an additional three species could not be confirmed. **Perlesta dakota, n. sp.,** is described from the adult male, female and egg. Diagnostic characters are presented using illustrations and a SEM photomicrograph.

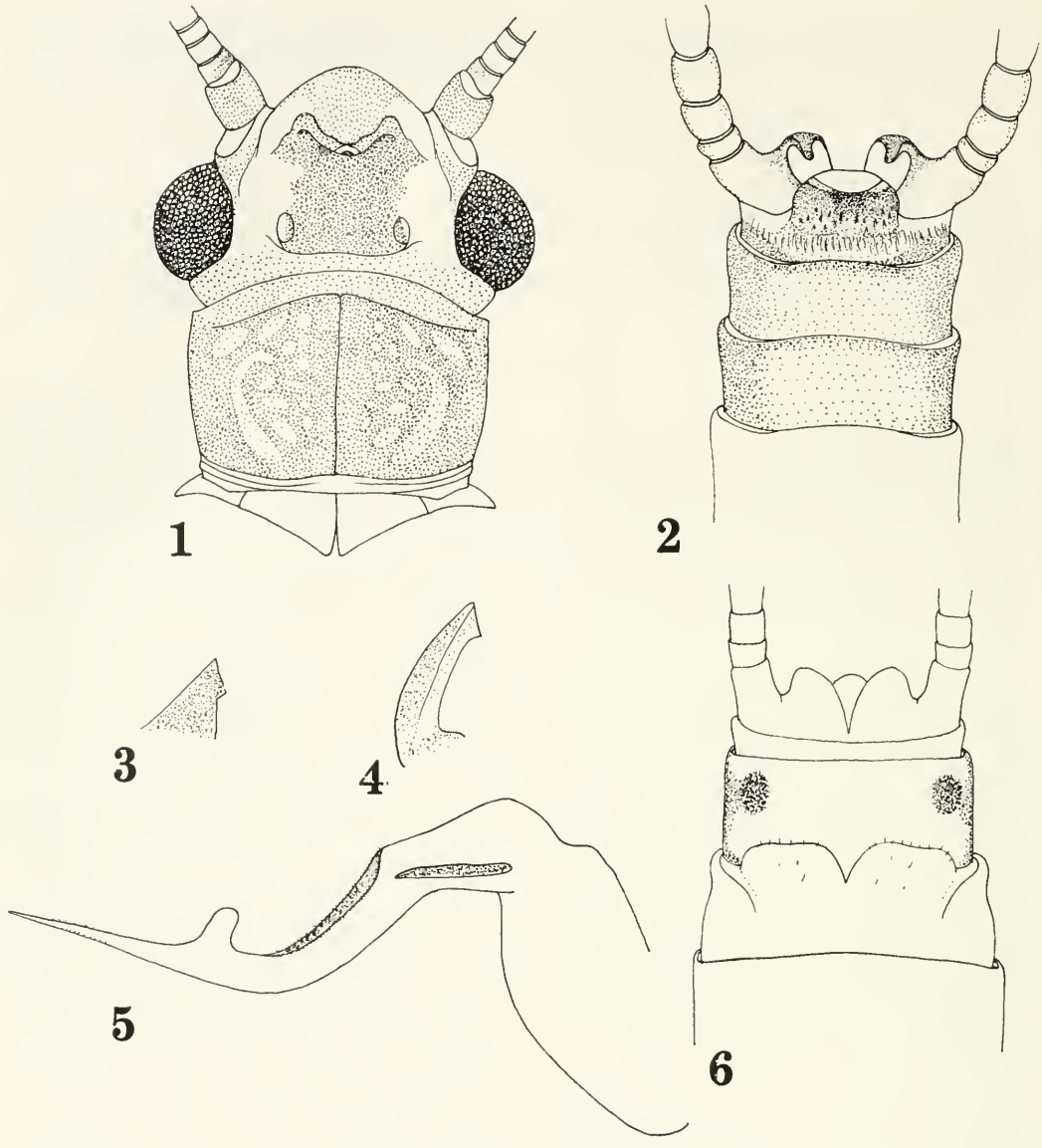
Key Words: stoneflies, Plecoptera, North Dakota, *Perlesta,* new species

Only two species of stoneflies were listed for North Dakota by Stark et al. (1986), a state covering 18,299,503 hectares that includes two major river systems, the Missouri and the Red River of the North. The landscapes of North Dakota, as common with most Northern Great Plains states, exhibit relatively little topography, and the state is better known for its numerous prairie marshes (Van der Valk 1989). Many counties of the state have 80–90% of their total area in agricultural production.

The Red River forms the eastern border of the state with Minnesota, traversing the former bed of the glacial Lake Agassiz. The area west of the Red River Valley, a region often referred to as the Drift Prairie is poorly drained, with few streams of any gradient. West of the Drift Prairie is the Missouri Plateau, also an area of poor drainage, and further west is the Missouri River and its associated tributaries. These streams are often located in broad valleys of native grasses or hay and small grain production areas. The Little Missouri River is a prominent feature of western North Dakota and drains through the spectacular landscape known as the "Badlands." Streams of the Badlands are mostly silty and relatively unproductive (Gordon and Post 1965). A southern extension of the Northern Coniferous Forest can be found in the northwestern portion of the state.

Despite the presence of suitable lotic habitats throughout the state, only nine species of stoneflies have been recorded from North Dakota. Stark et al. (1986) in their compilation of North American stonefly records, listed only *Strophopteryx fasciata* (Burmeister) and *Haploperla orpha* (Frison). However, we have found seven additional records in the literature. Harden and Mickel (1952) noted a record for *Isoperla longiseta* (Banks), and Neel (1985) in his ecological study of the Turtle River in eastern North Dakota discussed a species of *Acroneuria, Perlesta placida* (Hagen), and *Taeniopteryx nivalis* (Fitch). Finally, Stoaks (1975) listed nymphal records of *Pteronarcys dorsata* (Say), *P. placida, A. arenosa* (Pictet) and *I. bilineata* (Say) from the Forest River.

A recent collecting trip by the authors into southwestern North Dakota yielded an



Figs. 1–6. *Perlesta dakota.* 1, Adult head and pronotum. 2, Male terminalia, dorsal. 3, Paraproct, caudal. 4, Paraproct, lateral. 5, Penis. 6, Female subgenital plate, ventral.

undescribed species of *Perlesta.* The genus *Perlesta* in North America presently includes sixteen species (Stark 1989, Poulton and Stewart 1991, Stark and Rhodes 1997, Kirchner and Kondratieff 1997, DeWalt et al. 1998). The terminology in the description follows that proposed by Stark (1989).

Perlesta dakota Kondratieff and Baumann, new species

(Figs. 1–7).

Male.—Forewing length 8–9 mm. General color brown. Head yellow with dark brown pattern as Fig. 1. Pronotum dark brown (Fig. 1). Antennal scape and pedicel

brown, basal flagellular segments becoming darker brown beyond segments 10–16. Forefemur dorsally brown. Wing membrane and veins brown except costal margin pale. Abdominal terga brown, sterna yellow brown usually with darker brown triangle-shaped shading. Cercus yellow brown. Tergum 10 mesal sclerite not divided, sensilla basiconica small and scattered (Fig. 2). Paraproct short in caudal view (Fig. 3), more slender in lateral view (Fig. 4), spine anteapical and directed mesad (Figs. 2 and 3). Penis tube + sac moderately long with raised shelf dorsobasally; caecum prominent, dorsal hair patch broad basally narrowing to base of caecum, lateral hair patch elongate (Fig. 5). Female. Forewing length 10–12 mm. Color pattern similar to male but paler. Subgenital plate truncate with notch deep and narrowly V-shaped (Fig. 6).

Egg.—Collar button-like. Chorion surface finely pitted with scattered coarser pitting. Micropylar row in posterior region (Fig. 7).

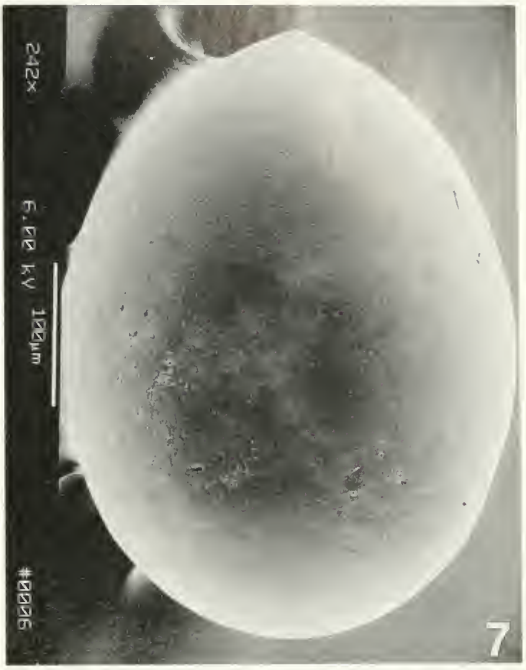


Fig. 7. *Perlesta dakota,* scanning electron photomicrograph of egg.

Nymph.—Unknown.

Types.—Holotype ♂, allotype ♀: North Dakota, Hettinger Co., Cannonball River, at New England, Hwy 22, 15 July 1997, R. W. Baumann and B. C. Kondratieff. Paratypes, same data as holotype: 14 ♂, 9 ♀; Ransom Co., Fort Ransom State Park, 11 July 1970, S. M. Anders, 1 ♂, 1 ♀ (NDSU); Stark Co., Heart River, Hwy 22, Dickinson, 14 July 1997, R. W. Baumann and B. C. Kondratieff, 2 ♀ (BYUC, CSUC). Holotype and allotype deposited in the National Museum of Natural History, Smithsonian Institution, other paratypes at the Monte L. Bean Life Sciences Museum, Brigham Young University (BYUC); C. P. Gillette Museum of Arthropod Diversity, Colorado State University (CSUC); North Dakota State University (NDSU) and the B. P. Stark Collection (BPSC).

Etymology.—The Sioux were the largest tribe of Native Americans of the North American Plains and prairies, and are called the Dakota in the Santee dialect.

Diagnosis.—*Perlesta dakota* appears similar to a group of dark species, including *P. cinctipes* (Banks), *P. adena* Stark, *P. fusca* Poulton and Stewart, and *P. xube* Stark and Rhodes. *Perlesta dakota* seems most similar to *P. fusca,* a species distributed throughout the Ozark-Ouachita Mountain region of Arkansas, Missouri and Oklahoma (Poulton and Stewart 1991). Males of *P. dakota* can be distinguished from *P. fusca* by the well developed thumb-like caecum (Fig. 5) and maculation of the head (Fig. 1). The penis structure of *P. dakota* is similar to *P. decipiens* (See Stark 1989; Figs. 42–43) but the former species can be distinguished by the dark brown wing and body coloration and head pattern. Females of *P. dakota* can be distinguished from *P. fusca* by the more truncate lobes of the subgenital plate and the deep and narrow notch (Fig. 6). The egg collar of *P. dakota* is button-like (Fig. 7), and the chorion finely pitted (Fig. 8). Poulton and Stewart (1991) indicated that the egg of *P. fusca* lacks a collar and the surface of the

egg is reticulate. The egg of *P. decipiens* has a distinctive short collar.

Remarks.—The type locality, the Cannonball River at New England, is typical of an agriculturally-impacted stream of the region, little or no riparian vegetation, heavily silted and with only few small riffles. Adults of *P. dakota* were collected by beating tall overhanging streamside grasses. Other aquatic insects collected with *P. dakota* include the damselfly *Calopteryx aequabilis* Say, the mayfly *Caenis* sp., and the caddisflies, *Cheumatopsyche pettiti* (Banks), *Ceratopsyche morosa* (Hagen), *Hydroptila consimilis* Morton, and *Limnephilius hyalinus* Hagen.

North Dakota Stonefly Records

Collections examined, primarily from North Dakota State University (NDSU), yielded new records or added to or substantiated previous records of North Dakota stoneflies. Other institutions listed include Brigham Young University (BYUC), Colorado State University (CSUC); Dickinson State University (DSUC); Minot State University (MSUM); Mississippi College (BPSC); Museum of Comparative Zoology, Harvard University (MCZC), University of Minnesota (UMSP), and University of Mississippi (UMIC). Some of these records are only identified to the generic level, but are included for distributional purposes, since so few stonefly records are currently available for North Dakota. A total of fifteen stonefly taxa are known from the state of North Dakota, representing at least eleven species.

Allocapnia sp.

Records.—Ransom Co., cold spring-fed stream, joining Sheyenne River, Hwy 46, Little Yellowstone Park, 1 Nov 1962, R. D. Gordon, 6 N (NDSU).

Several species of this genus of winter stoneflies could occur in North Dakota, especially *A. pygmaea* (Burmeister) (Ross and Ricker 1971).

Oemopteryx fosketti (Ricker)

Records.—Billings Co., Little Missouri River, Medora, 19 March 1997, C. P. Milne, 16 ♂, 6 ♀ (BYUC, CSUC, DSUC); Little Missouri River, Sully Creek Campground, 19 March 1997, C. P. Milne, 11 ♂, 1 ♀ (BYUC).

The species originally described from Saskatchewan, Canada, can be abundant in large and often silty rivers of the Missouri, Colorado, and Saskatchewan drainages (Baumann et al. 1977). Records for this species are known from nearby Dawson Co., Montana. The males have peculiar upturned forewing tips.

Strophopteryx fasciata (Burmeister)

Records.—Cass Co., Fargo, 24 April 1900, E. Cleveland, 1 ♂ (MCZC).

Strophopteryx fasciata is a widespread species occurring throughout eastern and midwestern North America, and typically a larger stream species emerging in late winter and early spring (Stewart and Stark 1988).

The record for *T. nivalis* by Stoaks (1975) could not be confirmed due to the lack of material, but is possible, since this species is common in Minnesota (Ricker and Ross 1968).

Pteronarcys pictetii Hagen

Records.—North Dakota: Cavalier Co., 20 Oct 1962, 2 N (NDSU); Pembina Co., Pembina River, Walhalla City Park, 1 July 1970, Perkins and R. L. Post, 1 ♀ (NDSU); Pembina River, Walhalla, 9 July 1961, R. L. Post and H. Osborn, 4 N (NDSU); same but 20 Oct 1962, E. Saugstad, 2 N (NDSU); Richland Co., Sheyenne River, 14 mi NW Walcott, 24 June 1963, D. Aarhus, 1 ♀ (NDSU).

Pteronarcys pictetii has been reported from adjacent Minnesota and Manitoba (Stark et al. 1986), and was expected in the state. The separation of the nymphs of *P. dorsata* (Say) and *P. pictetii* is difficult, especially immature specimens. The transcon-

tinental species, *P. dorsata* has been reported from all surrounding states and Canadian provinces except South Dakota (Stark et al. 1986).

Pteronarcys sp.

Records.—Cass Co., Stearn, 25 Aug 1960, 1 N (NDSU); Cavalier Co., 20 Oct 1962, 1 N (NDSU); Grand Forks Co., Turtle River State Park, 8 Aug 1962, R. D. Gordon, 2 N (NDSU); Forest River, Hwy 18, 3 mi NE Inkster, 1 July 1970, R. Stoaks, 1 N (NDSU); same but 25 Aug 1970, 1 N (NDSU); same but 19 June 1971, 1 N (NDSU); same but 28 Aug 1971, 3 N (NDSU); same but 15 Sept 1991, 3 N (NDSU); Ward Co., Mouse River, Nedrose #1, SE Minot, 13 July 1957, R. Nelson, 1 ♀ (MSUM).

The nymphs collected by Ralph D. Stoaks are apparently the specimens listed by him as *P. dorsata*, a species that remains unconfirmed for the state. The adult female listed above could not be determined to species.

Acroneuria abnormis (Newman)

Records.—Richland Co., Mirror Pool, Sheyenne River, 23 June 1975, P. K. Lago, 1 ♂ (UMIC).

This widespread species was expected in North Dakota, and is known from all surrounding states and Canadian provinces (Stark et al. 1986, Huntsman et al. 1999).

Acroneuria lycorias (Newman)

Records.—Cass Co., Sheyenne River, 5 mi E Kindred, 28 June 1996, K. Mundal, 2 ♂, 3 ♀ (NDSU), same but 30 June 1996, K. Mundal, 2 ♂, 3 ♀ (NDSU); Grand Forks Co., Forest River, Hwy 18, 3 mi NE Inkster, 16 Oct 1971, R. Stoaks, 1 N (NDSU); Pembina Co., Pembina River, Walhalla, 9 Sept 1961, R. L. Post and H. Osborn, 14 N (NDSU); same but 20 Oct 1962, E. Saugstad, 2 N (NDSU); same but 20 Oct 1996, D. G. Aarhus, 1 N (NDSU).

This widespread eastern and upper midwestern Nearctic species has been recorded from adjacent Minnesota and Manitoba. Harden and Mickel (1952) indicated that this species is one of the few stoneflies that occur in the western prairie regions of Minnesota.

Acroneuria sp.

Records.—Pembina Co., Pembina River, Walhalla, 9 Aug 1961, H. Osborn, 1 N (NDSU); Walsh Co., Forest River, USGS Gage, 3 mi SE Fordville, 15 Sept 1971, R. D. Stoaks, 1 N (NDSU).

Other possible species of *Acroneuria* reported from adjacent states and Canadian provinces include *A. carolinensis* (Banks) and *A. internata* (Walker) (Stark et al. 1986). Stoaks (1975) listed *A. arenosa*, however, this nymphal determination is doubtful since this species is restricted to the eastern U.S. (Stark and Gaufin 1976).

Perlesta decipiens (Walsh)

Records.—Cass Co., Sheyenne River, 5 mi E Kindred, 28 June 1996, K. Mundal, 3 ♀ (NDSU); NDAC, Fargo, USDA UV light trap, 6 July 1956, 1 ♀ (NDSU); Richland Co., 13 July 1962, 1 ♂, 4 ♀ (NDSU); Trail Co., Elm River, 8 Aug 1969, R. L. Post, 1 ♂ (NDSU).

The occurrence of this geographically widespread species was expected in the state.

Perlesta xube Stark and Rhodes

Records.—Walsh Co., Forest River, Hwy 35, 8 July 1966, R. L. Post, 2 ♂, 2 ♀, 3 N (NDSU).

Perlesta xube was recently described from a small stream in Cherry County, Nebraska (Stark and Rhodes 1997). This record from the Forest River represents a northeastern range extension, indicating that this species may occur in remnant stream systems throughout the northern Great Plains.

Perlesta sp.

Records.—Cass Co., Fargo, 13 July 1973, P. K. Lago, 1 ♀ (UMIC); Dunn Co.,

Knife River, Manning, 29 May 1991, Mott, 1 N (DSUC); Grand Forks Co., Turtle River, 23 June 1970, D. M. Huntsinger, 1 N (NDSU); Forest River, Hwy 18, 3 mi NE Inkster, 23 June 1970, R. D. Stoaks, 4 N (NDSU); Slope Co., Burning Coal Vein, 0.25 mi W Logging Camp Ranch, Little Missouri National Grassland, 6 July 1968, R. D. Stoaks, 6 N (NDSU); Walsh Co., Forest River, 3.5 mi W Fordville, Hwy 32, 19 June 1971, R. D. Stoaks, 31 N (NDSU); same but 11 July 1971, R. D. Stoaks, 4 N (NDSU); same but at USGS gage, 19 May 1971, R. D. Stoaks, 1 N (NDSU).

Nymphs of *Perlesta* are difficult to specifically distinguish, and much of the above material is poorly preserved or represents early instars. Stoaks (1975) and Neel (1985) reported *P. placida* as nymphs and as nymphs and adults, respectively. Stark (1989) determined that *P. placida* was a complex of at least twelve (now sixteen) species. No adults from Neel (1985) were available for study. With no associated males, the single female adult from Fargo was left undetermined.

Isoperla bilineata (Say)

Records.—Cass Co., Fargo, NDSU Campus, 7 June 1963, R. W. Poole, 7 ♂, 1 ♀ (NDSU); same but 16 June 1963, R. W. Poole, 7 ♂, 1 ♀ (NDSU) same but 18 June 1993, 6 ♂ (NDSU); Sheyenne River, 5 mi E Kindred, 30 June 1996, K. Mundal, 1 ♂, 4 ♀ (NDSU); NDAC, Fargo, USDA UV light trap, 9 June 1956, 20 ♂, 3 ♀ (NDSU). Emmons Co., 16 mi W Linton, 20 June 1975, P. K. Lago, 2 ♂ (UMIC); Grant Co., Heart Butte Dam, 19 June 1975, P. K. and B. A. Lago, 2 ♂ (UMIC); Pembina Co., Tongue River, Kotchman Farm, near Cavalier, 29 June 1974, P. K. and B. A. Lago, 3 ♂ (UMIC); same but 2 July 1975, 2 ♂ (UMIC).

Stoaks (1975) previously reported this species, but no specimens from his study were available for examination. Szczytko and Stewart (1978) indicated material from the Red River of the North, Minnesota, which forms the border with North Dakota.

Isoperla longiseta (Banks)

Records.—Billings Co., Little Missouri River, Elkhorn Ranch, 20 June 1965, R. L. Post, 1 ♀ (NDSU); Cass Co., Fargo, 11 May 1939, D. G. Denning, 1 ♀ (UMSP); Slope Co., Little Missouri River, at Marmarth, Hwy 12, 14 July 1997, R. W. Baumann and B. C. Kondratieff, 6 ♂, 7 ♀ (BYUC, CSUC).

Isoperla longiseta is known from western and midwestern North America, and occurs further east than any other typically western *Isoperla* (Szczytko and Stewart 1979). It is often considered a typical prairie stonefly of larger streams and rivers (Harden and Mickel 1952, Ricker 1946, 1964). Harden and Mickel (1952) previously mentioned the 1939 record of *I. longiseta* from Fargo.

Haploperla orpha (Frison)

Records.—Pembina Co., Tongue River, Kotchman Farm near Cavalier, 21 June 1974, P. K. and B. A. Lago, 2 ♂, 3 ♀ (BPSC); same but 23 July 1975, 1 ♂, 3 ♀ (UMIC).

Haploperla orpha is a relatively poorly known species having also been recorded from Maine, Minnesota, Quebec, New Brunswick, and Wisconsin (Stark et al. 1986). Typically, nymphs of this species are found in medium and small-sized streams with some gradient.

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A NEW NEARCTIC SPECIES OF *LESTODIPLOSIS* (DIPTERA: CECIDOMYIIDAE) PREYING ON AN OAK LEAF TIER, *PSILOCORSIS QUERCICELLA* (LEPIDOPTERA: OECOPHORIDAE)

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Abstract.—A new species of cecidomyiid, ***Lestodiplosis venusta* Gagné,** is described, illustrated, and compared to its most similar congeners. Larvae of the new species were found in Missouri preying on caterpillars of *Psilocorsis quercicella* Clemens, a leaf skeletonizer of oaks. An unidentified species of Ceraphronidae was reared from pupae of the *Lestodiplosis.*

Key Words: *Lestodiplosis,* predator, oak leaf tier

A new species of *Lestodiplosis* attacking larvae of the oecophorid *Psilocorsis quercicella* Clemens was discovered by one of us (JTL) during the course of an ecological study of the natural enemies of the lepidopteran in Missouri. *Psilocorsis quercicella* is a common bivoltine moth found throughout eastern United States (Covell 1984). The larvae skeletonize the surface of oak leaves within leaf shelters formed by tying together adjacent oak leaves with silk. Larvae of the gall midge predator appear to be highly mobile ectoparasites of early instar *P. quercicella* larvae and are often gregarious. When present, one to four of the predaceous cecidomyiids were found per caterpillar. The predator was found feeding on *P. quercicella* on both white oak (*Quercus alba* L.) and black oak (*Q. velutina* Lam.). After feeding, full grown *Lestodiplosis* larvae spin a silken cocoon within the leaf shelter, often incorporating pieces of caterpillar frass onto the surface of the cocoons. To date, larvae of the predator have been observed only from second generation *P. quercicella* larvae collected in late summer and fall in Missouri. An unidentified gregarious parasitoid (Hymenoptera: Ceraphonidae) has been reared from the *Lestodiplosis* pupae.

The genus *Lestodiplosis* contains some 175 known species in the world that attack many kinds of insects and mites. Some appear to be specialist predators, others are evidently generalists. Many species are known from only one or a few specimens so it is especially helpful to have several series of the same species from a particular niche, such as JTL found in leaf ties of *P. quercicella.*

METHODS

Larvae of the predator were reared to the adult stage in 16-oz. closed clear plastic containers kept at 23°C and with a photoperiod of 14:10 (L:D) h. Humidity was maintained with moist filter paper. Specimens of immature stages and reared adults were preserved in 70% isopropyl alcohol. Specimens were mounted on microscope

slides using the method outlined in Gagné (1989). Terminology for adult morphology follows usage in McAlpine et al. (1981) and for larval morphology that in Gagné (1989).

Lestodiplosis venusta Gagné, new species
(Figs. 1–13)

Adult.—*Head:* Eyes connate, 11–12 facets long at vertex; facets hexagonal, all closely adjacent. Occiput with dorsal protuberance. Frons with 10–14 setae. Labella hemispherical but pointed apically, each with several lateral setae. Palpus 4-segmented. Male antennal flagellomeres (Fig. 1) binodal; basal node and the distal third of the neck dark; one circumfilum on the basal node, two on the distal, the loops of the three circumfila unequal in length; the proximal and distal circumfila with ventralmost loops greatly elongated and much longer than remaining loops. Female flagellomeres (Fig. 2) with basal part of node and distal part of neck darker than remainder of flagellomere; circumfila with some short loops.

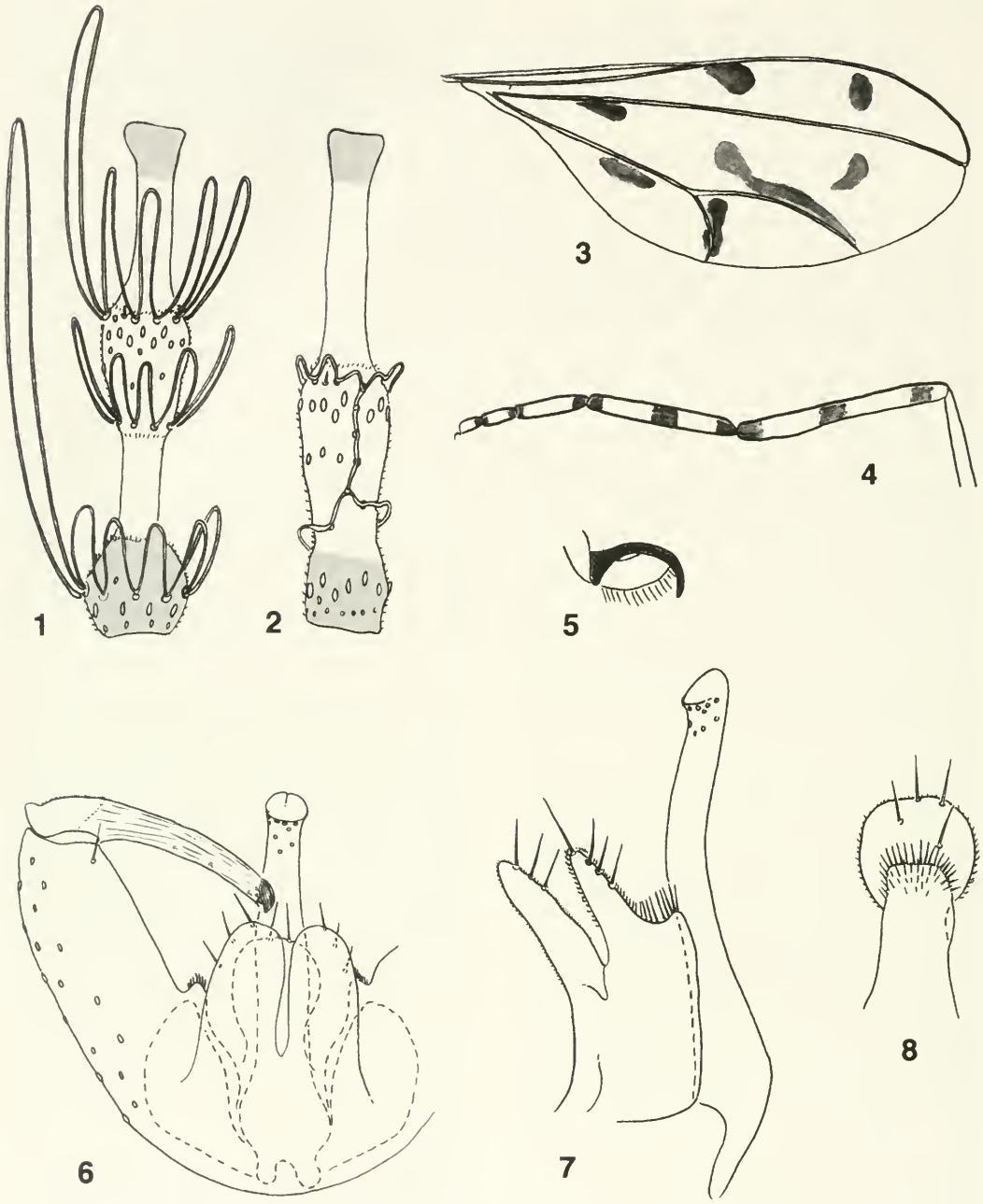
Thorax: Wing (Fig. 3) 1.8–2.3 mm long, R_5 slightly curved, joining C posterior to wing apex; 7–8 irregular dark spots present on wing. Legs (Fig. 4) with alternating light and dark groups of scales. Tarsal claws (Fig. 5) untoothed, curved beyond midlength; empodia attaining bend in claws.

Male abdomen: First through seventh tergites entire, rectangular, with single posterior row of setae, several lateral setae, scattered scales, and 2 anterior trichoid sensilla; eighth tergite undifferentiated, the only vestiture the anterior pair of trichoid sensilla. First through seventh sternites quadrate, with single to double posterior row of setae, scattered setae elsewhere, no scales, and 2 anterior trichoid sensilla; eighth sternite similar to preceding except weakly sclerotized anterolaterally. Genitalia (Figs. 6–8): cerci each with rounded posterior margin; hypoproct simple, rounded at apex, as long as but slightly wider in ventral view than cerci, with 2 pairs of apicoventral setae, produced anteroventrally into large lobe lying in close juxtaposition with dorsal surface of aedeagus and covered posteriorly with short spinules; aedeagus elongate with blunt apex, sinuous in side view; gonocoxite elongate cylindrical with short, triangular mesobasal lobe bearing short spinules; gonostylus elongate cylindrical, with setulae near base and covered with minute carinae and only several short setae beyond.

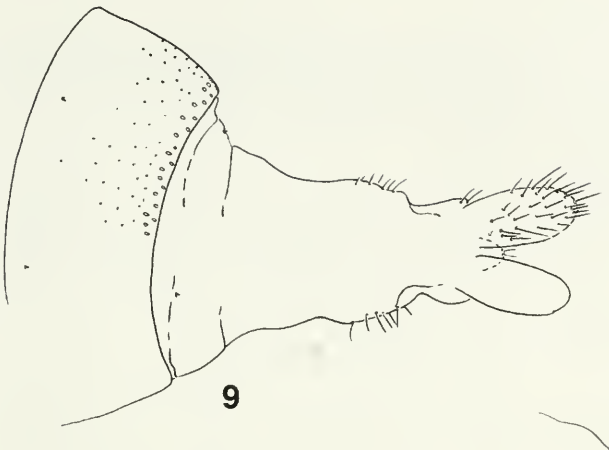
Female abdomen (Figs. 9–11): First through seventh tergites entire, rectangular, with mostly single row of posterior setae, several lateral setae, extensively covered with scales, and 2 anterior trichoid sensilla. Second through seventh sternites quadrate, extensively covered with setae and scales and with anterior pair of trichoid sensilla. Eighth segment much narrowed, without differentiated tergite and sternite, the tergum with anterior pair of trichoid sensilla the only vestiture, the sternum with anterior pair of trichoid sensilla and covered with setae some distance beyond. Tenth segment without vestiture dorsally, with scattered setae ventrally; cercus large, ovoid, with ventral field of short, closely-set, sensory setae, and scattered setae elsewhere. Hypoproct short, wide, the convex posterior edge with 2 short setae. Apex of ninth sternite protruding posteriorly below hypoproct, rigid, triangular.

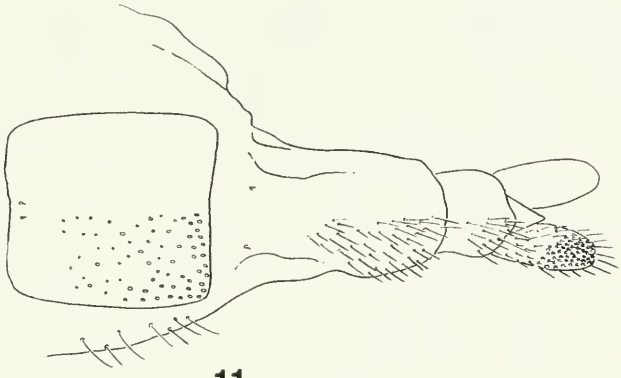
Third larval instar (Figs. 12–14).—Integument mostly smooth, 2 pseudopods present ventrally on mesothorax and metathorax and 3 each on first through seventh abdominal segments. Antenna much longer than wide. Cephalic apodemes slightly longer than head capsule. Spatula absent. Lateral papillae in 2 groups of 3 on each side of central line, only one setose in each group. Second and fifth dorsal papillae of each segment much shorter than remaining four. Terminal segment with 6 elongate setae, usually with expanded apices.

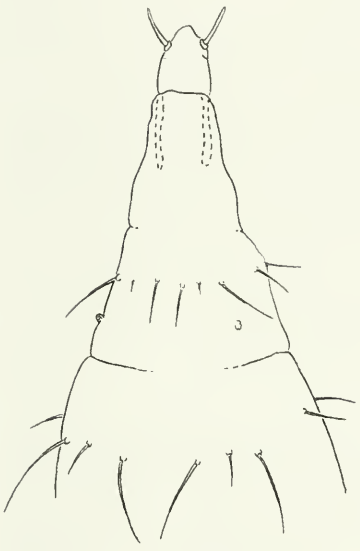
Holotype.—♂, reared from larva preying on larva of *Psilocorsis quercicella* on oak, Cuivre River State Park, Troy, Missouri, 1-IX-1997, J. Lill, deposited in the National

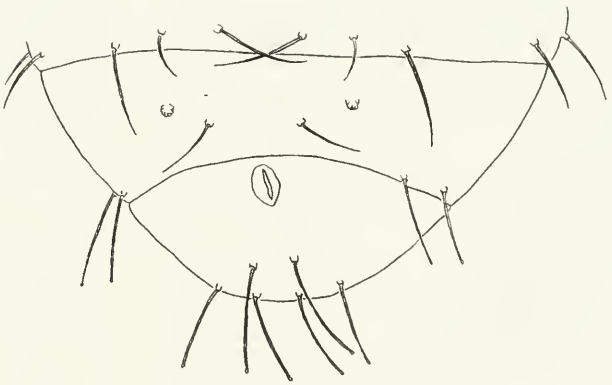


Figs. 1–8. *Lestodiplosis venusta*. 1, Male third antennal flagellomere. 2, Female third antennal flagellomere. 3, Wing. 4, Foreleg. 5, Tarsal claw and empodium. 6, Gonopod, cerci, hypoproct, and aedeagus (dorsal). 7, Cercus, hypoproct, and aedeagus (lateral). 8, Hypoproct (ventral).









Figs. 9–14. *Lestodiplosis venusta*. 9–11, Female postabdomen. 9, Seventh tergite to cerci (not all setal bases and setae indicated; dorsal). 10, Cerci, hypoproct and apex of ninth sternum, the postabdomen retracted (lateral). 11, Seventh sternite to cerci (not all setal bases and setae indicated; ventral). 12–14, Larva. 12, Head, neck, and first two thoracic segments (dorsal). 13, part of mesothorax with two groups of three lateral papillae, a ventral papilla, and two pseudopods (ventrolateral). 14, Apex of seventh and all of eighth and terminal abdominal segments (dorsal).

Museum of Natural History (USNM), Washington, DC.

Other material examined.—All associated with leaf ties of *Psilocorsis quercicella,* Cuivre River State Park, Troy, Missouri: 6 ♂, 5 ♀, 9 larvae, same data as holotype; 6 ♂, 1 ♀, same data as holotype except collected 11-IX-1996, all in USNM.

Etymology.—The specific name, *venusta,* is an adjective meaning beautiful, with reference to the striking black and white banded legs and antenna.

Remarks.—The banded antenna and legs and the spotted wings of this species are generally similar to some other *Lestodiplosis* species, but the combination of unequal male circumfila and a blunt-tipped aedeagus is characteristic in the Nearctic Region of a narrower group of three species that differ chiefly in details of the male genitalia. These three species are: *Lestodiplosis florida* Felt, *Lestodiplosis cinctipes* (Felt), and *Lestodiplosis satiata* Felt. These other species are now under investigation by one of us (RJG) for a revision in progress of Nearctic *Lestodiplosis.*

Compared to the new species, the ventral hypoproctal lobe of *L. florida* is covered by fewer but more robust spinules and its aedeagus is much wider on the basal two-thirds and tapers abruptly to a narrow neck. *Lestodiplosis florida* was originally taken from a leaf roll on a *Crataegus* in Florida. This species is represented in the USNM collection by a specimen from Florida that was reared from galls on *Croton linearis* Jacq. and another that was swept from *Tsuga canadensis* (L.) Carr. in Ontario.

The ventral lobe of the hypoproct of both *L. cinctipes* and *L. satiata* is covered more extensively and by finer spinules than in the new species and the aedeagus in these species is narrower throughout its length than on *L. venusta.* In addition, the antennal circumfila loops of both species are all much longer than in *L. venusta.* Both species were originally caught in flight in New York, but a specimen of *L. satiata* in the USNM was reared in association with cynipine leaf galls on *Quercus* sp. in Pennsylvania and another was reared from flower heads of *Borrichia frutescens* (L.) DC. in North Carolina.

There is one other Nearctic *Lestodiplosis* species, besides *L. venusta,* that has been recorded as feeding on caterpillars. Felt (1933) described *Lestodiplosis novangliae* Felt from specimens associated with a tortricid *Epinotia* "*nanana*" on spruce in Massachusetts. He noted also that larvae similar to that species were found on another tortricid, *Rhyacionia* sp. on pine. The gonocoxites of *L. novangliae,* unlike those of *L. venusta,* have prominent and spiny mesobasal lobes.

Acknowledgments

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DESCRIPTION OF TWO NEW SPECIES OF *AMBLYCERUS* THUNBERG (COLEOPTERA: BRUCHIDAE) WITH A PROBABLE STRIDULATORY MECHANISM

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Abstract.—***Amblycerus atypicus,* new species,** and ***A. ischiodontus,* new species,** are described and illustrated. The former has an area with overlapping scales in part of the external elytral margins and the inner distal portion of the hind femur with fine transverse striation. *Amblycerus ischiodontus* has an area transversely striate on the metepisternum and an apical tooth on the ventral margin of the hind femur. The areas on the elytra and metepisternum probably act as a file and the striate area or the tooth of the hind femur as the scraper. The elytro-femoral method of stridulation is postulated for the first time in Bruchidae and is shared with *Amblycerus cistelinus* (Gyllenhal), *A. jatayensis* (Pic), *A. sosia* Ribeiro-Costa and Kingsolver, *A. whiteheadi* Kingsolver and *A. guazumicola* Kingsolver and Johnson. The other kind, involving the metepisternum and hind femur, has already been described for three other *Amblycerus* species: *A. eustrophoides* (Schaeffer), *A. pollens* (Sharp), and *A. stridulator* Kingsolver, Romero N., and Johnson. A key for the bruchid species with modified body areas probably involved in stridulation is presented.

Key Words: *Amblycerus,* stridulation, taxonomy, Bruchidae

Kingsolver (1970) first recorded the presence of areas of the integument probably involved in stridulation in Bruchidae. He indicated the presence of a fusiform node with transverse striations on the metepisternum and the presence of an apical blunt tooth on the ventral margin of the hind femur for *Amblycerus eustrophoides* (Shaeffer), which has a distribution restricted to North America. Kingsolver et al. (1993) noticed the same stridulatory areas for *A. stridulator* described from Mexico, Costa Rica, and Venezuela and for *A. pollens* (Sharp) recorded from Belize, Costa Rica, and Brazil.

Amblycerus atypicus, n. sp. (French Guiana), has an area with overlapping scales on the external margins of the elytra and fine transverse striation on the inner distal portion of the hind femur. The other new species, *Amblycerus ischiodontus* (Brazil), has the metepisternum and hind femur with areas transversely striate, similar to those mentioned for *A. eustrophoides, A. pollens,* and *A. stridulator.* These areas for each species are in contact when the hind leg is moved, and, even though no sound emission has been perceptible from dead specimens, it is possible that they form a stridulatory mechanism. Since males and females of both species have these areas, I hypothesize that the mechanism probably is not related with courtship behavior.

The type of stridulation in *A. atypicus* can be characterized as the elytro-femoral method, established by Dumortier (1963). The area with overlapping scales on the elytron would be the "pars stridens" (file)

and the striate area of the hind femur, the "plectrum" (scraper). Dumortier (1963) cited the presence of the elytro-femoral method for the Coleopteran families Scarabaeidae, Lucanidae, Cerambycidae, Cicindelidae, Tenebrionidae, and Carabidae. This method of stridulation is hypothesized for the first time in Bruchidae and is shared with the following *Amblycerus* Thunberg species: *A. cistelinus* (Gyllenhal), *A. jatayensis* (Pic), *A. sosia* Ribeiro-Costa and Kingsolver, *A. whiteheadi* Kingsolver, and *A. guazumicola* Kingsolver and Johnson.

The methodology used for the descriptions follows Ribeiro-Costa (1997).

Amblycerus atypicus Ribeiro-Costa, new species

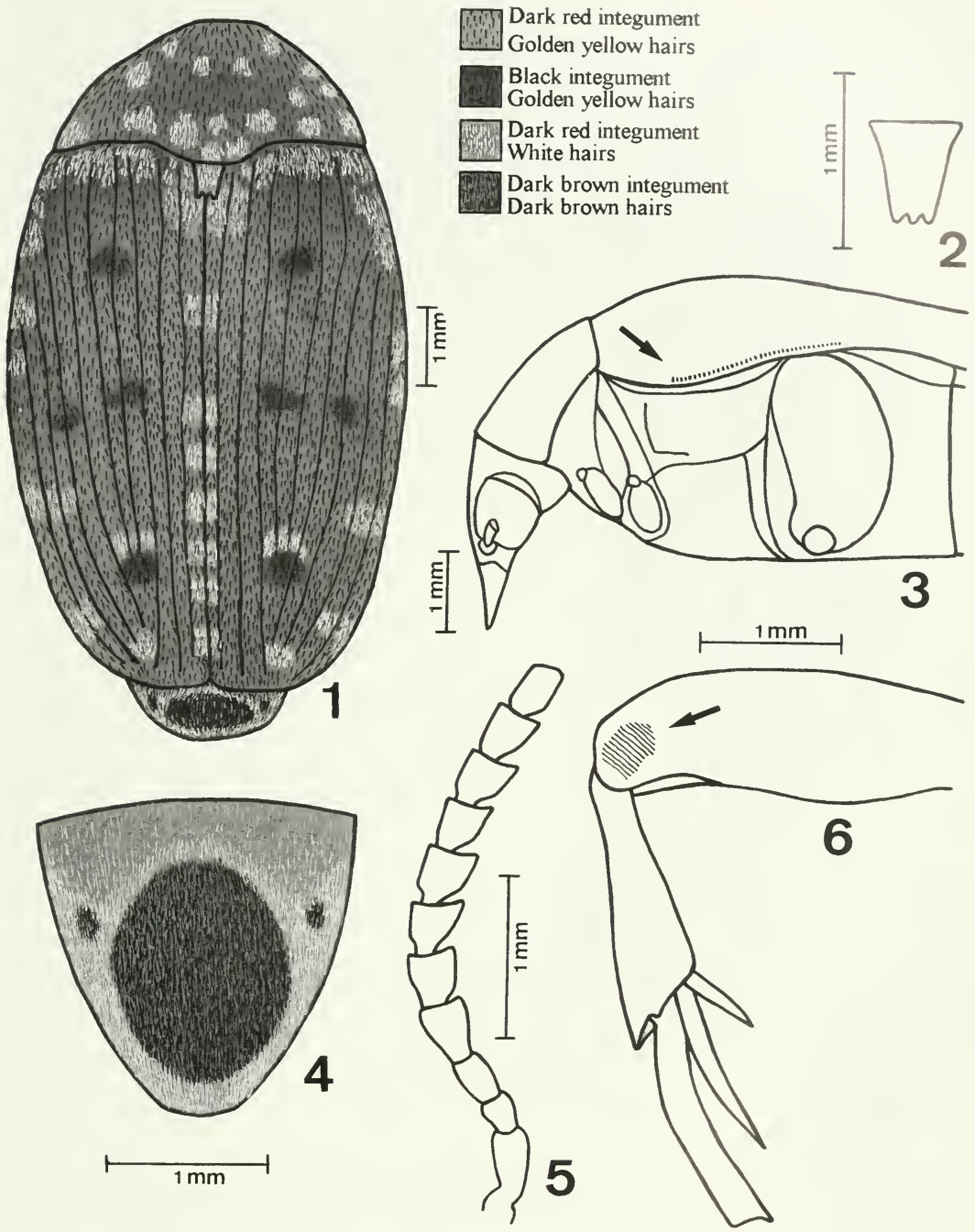
(Figs. 1–10)

Description.—*Measurements (pronotum + elytra):* Length 8.17–8.83 mm; width 4.83–5.17 mm.

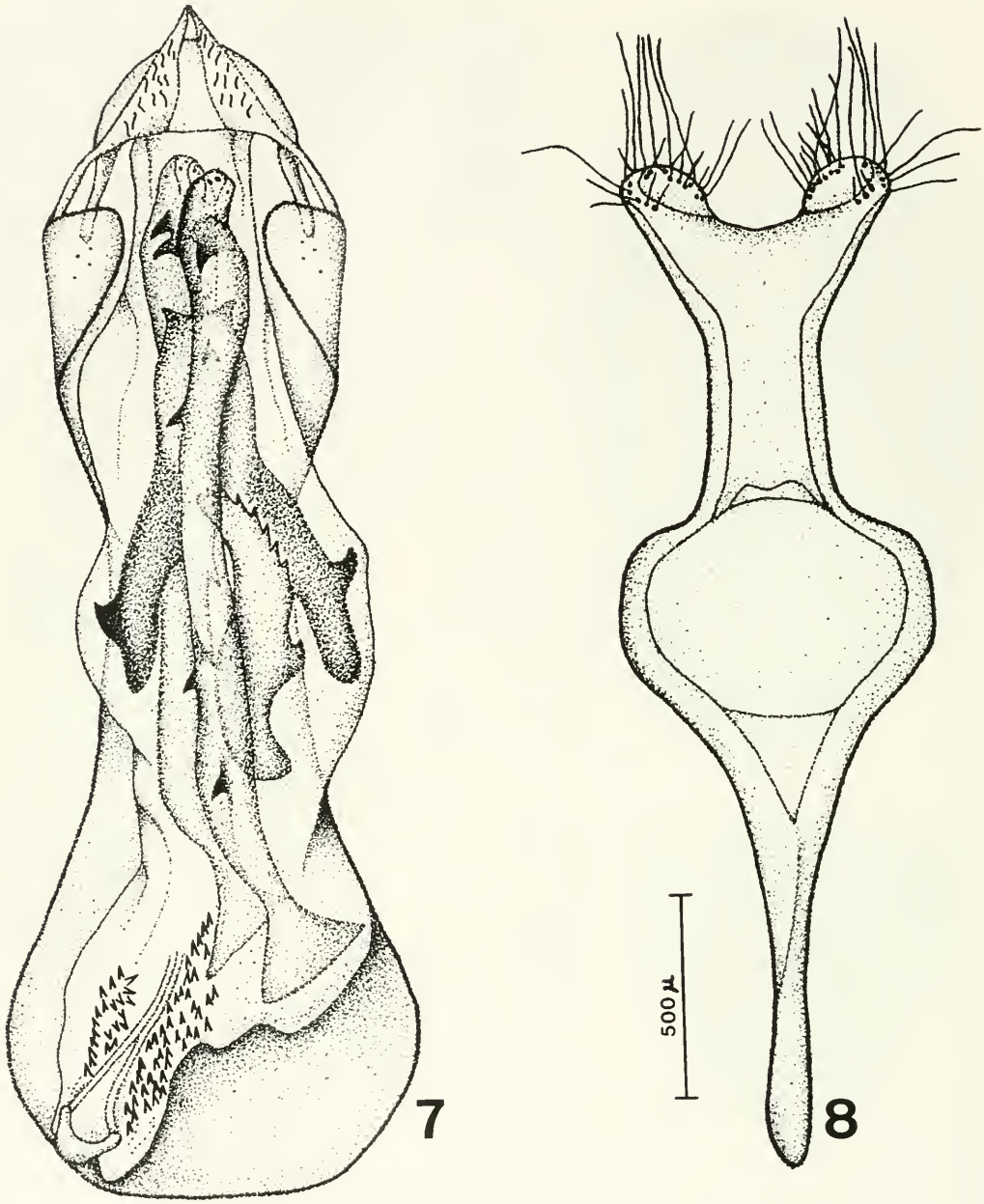
Integument: Antenna dark red. Dorsal surface (Fig. 1) dark red with scattered black spots on elytra, two on basal one-third, four at middle one-third and two on apical one-third. Lateral margins of elytra gently darker. Undersurface and legs dark red. Pygidium with large, ovate, central, dark brown spot (Fig. 4).

Vestiture: General coloration on dorsal surface golden yellow (Fig. 1). Pronotum with white setae forming six small, round spots arranged in triangle in middle lateral and scattered patches along basal lobe (Fig. 1). Scutellum usually white. Elytra (Fig. 1) with white setae in scattered patches along basal margin and around scutellum, often in a few small, irregular spots on median and external margins, in lines along interstitial margins and strial sulci, and condensed into a few, very small irregular patches on remainder of elytra. Pygidium (Fig. 4) with large, ovate, velvety dark brown spot, bordered with dense white setae and with two small patches of dark brown pillosity in anterolateral areas. Undersurface gently mottled brown and white. Lateral margins of abdominal sterna with white setae gently condensed into round patches.

Frons slightly flat, evenly punctate except on frontal carina. Eyes moderately faceted (3 ommatidia), protruding laterally; ocular index 3.9; ocular sinus 1/3.8 diameter of eye in lateral view; postocular lobe 1/9.5 times largest length of eye in lateral view. Antenna (Fig. 5) serrate from fourth to tenth segments, all gently longer than wide (1.1 times); last segment elliptical. Pronotum trapezoidal with lateral margins slightly arched in dorsal view, cervical sulcus present in lateral third, a sulcus outlining the emargination of basal lobe; long lateral carina, nearly reaching apex of pronotum, not forked anteriorly; surface densely punctulate, lateral one-third on either side also coarsely punctate. Prosternal process wide, margins sulcate, apex subacute, moderately expanded exceeding fore coxae and fitting into sulcate mesosternum. Scutellum (Fig. 2) about 1.9 times as long as wide, with tridentate apex. Elytra slightly convex in cross section along elytral suture, with an area with overlapping scales in part of the external margins (Fig. 9), truncated apically and with striae strongly impressed. Metepisternum with some punctures moderately, sparsely coarser; transverse axis of metepisternal sulcus (Fig. 3) strongly divergent from metapleural suture, very short longitudinal axis, less than half metepisternal length, not modified in a fusiform node with transverse striations (Fig. 3). Hind coxa with punctures moderately coarse and slightly dispersed, except in basal third. Hind femur (Fig. 6) 2.8 times as long as wide; apical tooth on ventral margin absent; internal face on distal portion with transverse striations (Figs. 6, 10). Hind tibia (Fig. 6) with coronal teeth approximately of same size; lateral spur 2.9 times length of median, first hind tarsal segment about 1.2 times as long as lateral spur and 3.6 times median spur; ventral face slightly convex with inconspicuous lines of punctures and setae in margins. Male pygidium vertical in lateral view, female oblique; male eighth



Figs. 1–6. *Amblycerus atypicus*. 1, Dorsal habitus. 2, Scutellum. 3, Lateral view of head and thorax. 4, Pygidium. 5, Antenna. 6, Hind leg.



Figs. 7–8. *Amblycerus atypicus*. 7, Male terminalia, median lobe. 8, Same, tegmen and lateral lobes.

tergite acute. Fifth visible abdominal sternum of female longer than that of male at middle, margin in both sexes entire.

Male terminalia (Figs. 7, 8): Eighth tergite acute apically. Median lobe (Fig. 7) with length 4.2 times its largest width in basal area; ventral valve moderately long, acute apically, with straight lateral margins; dorsal valve rounded. Basal area of internal sac (Fig. 7) without anterior and median sclerites; a pair of posterior tooth-like sclerites. Median region of internal sac (Fig. 7)

with two central, long laminar sclerites each with angulate apical portion and each one with one or two teeth near base, one subbasal and two on median portion; pair of sclerites laterad to laminars, longer than wide, each with one small curved tooth directed upward; unpaired median sclerite, 0.3 times as long as laminars, slightly sinuate in lateral view, with one side serrate. In apical area of internal sac (Fig. 7) one sclerite with long stems among many denticles. Tegmen with shallow emargination among enlarged lateral lobes (Fig. 8).

Discussion.—Romero et al. (1996) established the *cistelinus* group including *A. cistelinus*, *A. sosia*, and *A. guazumicola* mainly considering both the integument and pubescence pattern on the dorsal surface, not mentioning the presence of areas on elytra or hind femur possibly involved in stridulation. *Amblycerus atypicus* (French Guiana), *A. jatayensis* (Brazil) and *A. whiteheadi* (Panama, Nicaragua, Costa Rica, Colombia), probably will be included in this group (revisionary study currently underway) because they share characters cited by Romero et al. (1996) and also the areas on the external margins of the elytra with overlapping scales (Fig. 9) and transverse striation on the inner distal portion of hind femur (Fig. 10), which are apparently stridulatory in function.

Amblycerus atypicus is clearly separated from all the other *Amblycerus* species and especially from those in the *cistelinus* group by the form, number and arrangement of sclerites in the male internal sac (Fig. 7).

Types.—Holotype ♀. FRENCH GUIANA: Maroni River; Collection Wm Schaus, deposited in the National Museum Natural of History, Smithsonian Institution, Washington, D.C. U.S.A. One paratype ♂ with same label deposited in the Coleção de Entomologia Pe. Jesus S. Moure, Curitiba, Brazil.

Etymology.—The species name refers to the atypical elytro-femoral method of possible stridulation in *Amblycerus*.

Amblycerus ischiodontus Ribeiro-Costa, new species

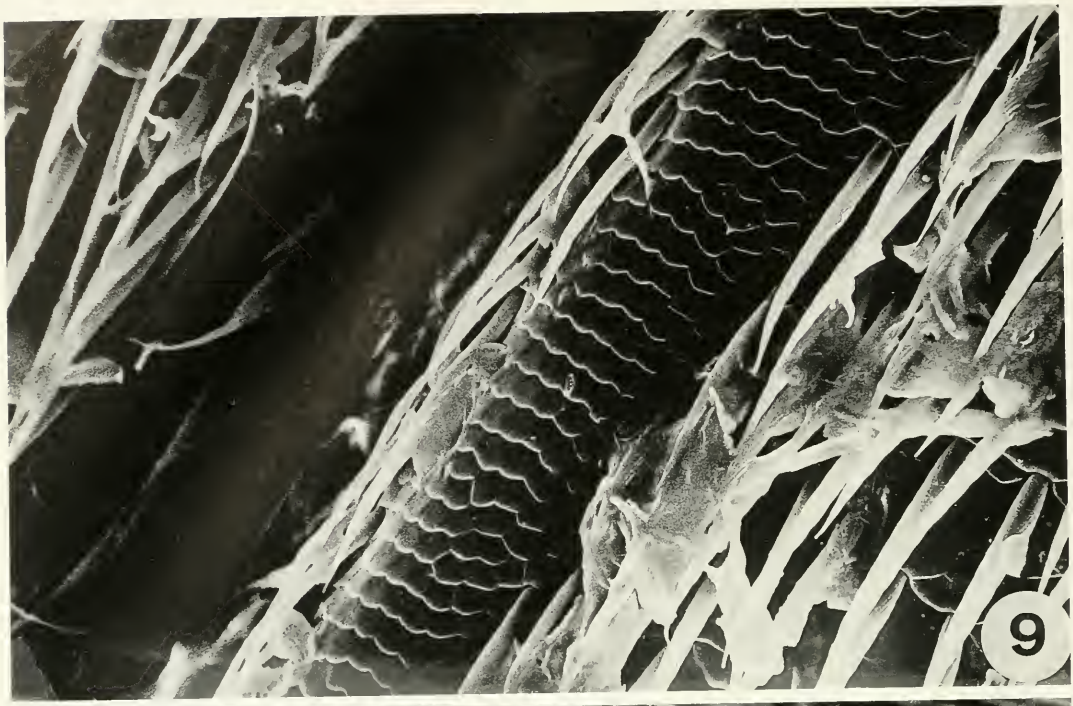
(Figs. 11–18)

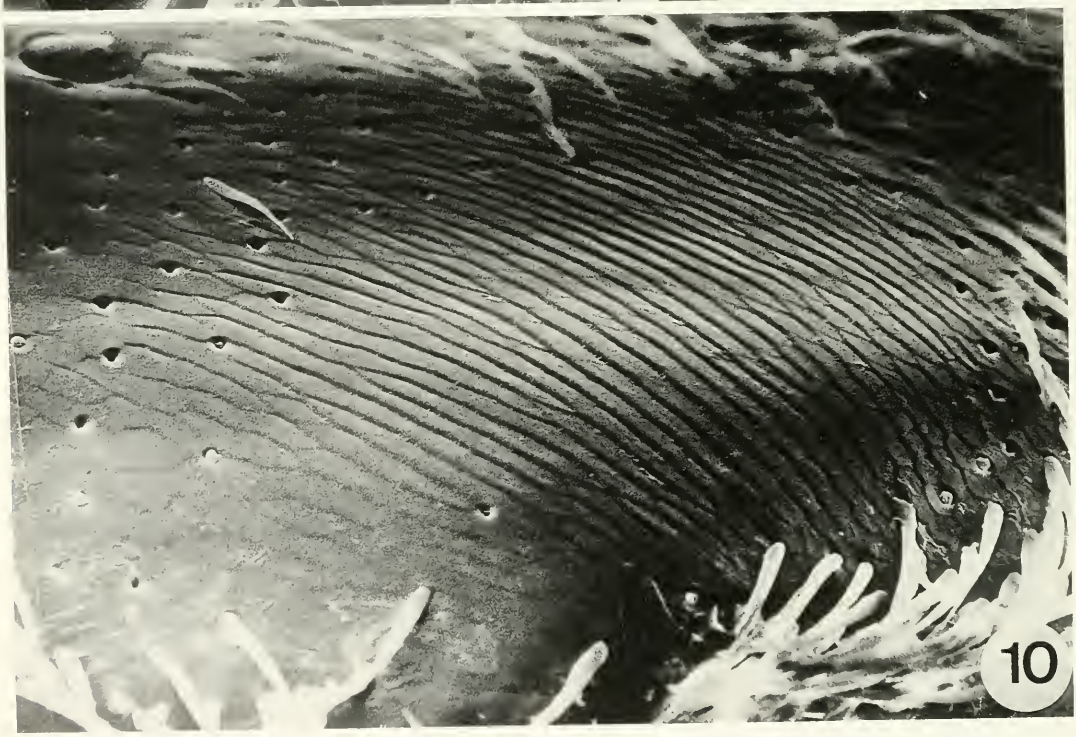
Description.—*Measurements (pronotum + elytra):* Length 4.48 mm; width 2.72 mm.

Integument: General coloration, dark red. Eyes, legs and undersurface of thorax darker.

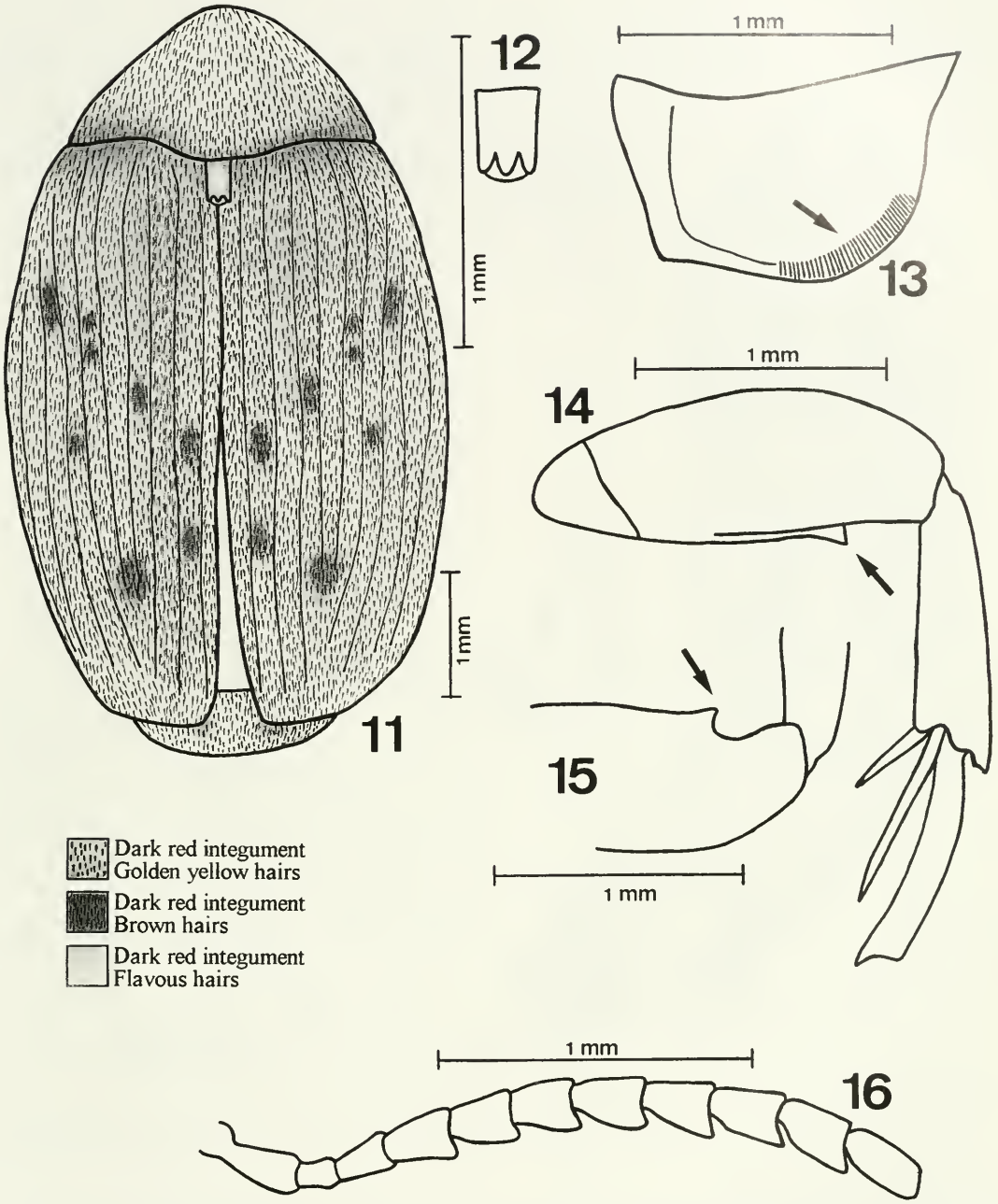
Vestiture: Head, appendages and ventral area of thorax and abdomen, flavous; metepisternum in part, golden yellow. Pronotum (Fig. 11) golden yellow rarely with small brown patches. Scutellum flavous. Elytra (Fig. 11) golden yellow; brown hairs in rare irregular patches and flavous hairs in lines along interstitial margins and strial sulci. Pygidium (Fig. 11) golden yellow with two small central, brown patches.

Frons slightly flat, evenly punctuated, frontal carina absent. Eyes moderately faceted (7 ommatidia), protruding laterally; ocular index 3.8; ocular sinus 1/5.0 diameter of eye in lateral view; postocular lobe 1/6.7 times largest length of eye in lateral view. Antenna (Fig. 16) serrate from fourth to tenth segments, all perceptibly longer than wide (1.4 times), last segment subelliptical. Pronotum trapezoidal with lateral margins moderately arched in dorsal view, cervical sulcus in lateral thirds and a sulcus outlining basal lobe; long lateral carina, nearly reaching apex of pronotum, not forked anteriorly; surface densely punctulate, lateral one-third either side also coarsely punctate. Prosternal process wide, not sulcate, apex subacute, moderately expanded between anterior coxae and fitting into sulcate mesosternum. Scutellum (Fig. 12) about 1.8 times as long as wide, apex strongly tridentate on rounded base. Elytra slightly convex in cross section along elytral suture, subtruncated apically and with striae strongly impressed. Transverse axis of metepisternum (Fig. 13) moderately divergent from metapleural suture; transversely striate and strongly curved area running with longitudinal axis, apparently being a modification



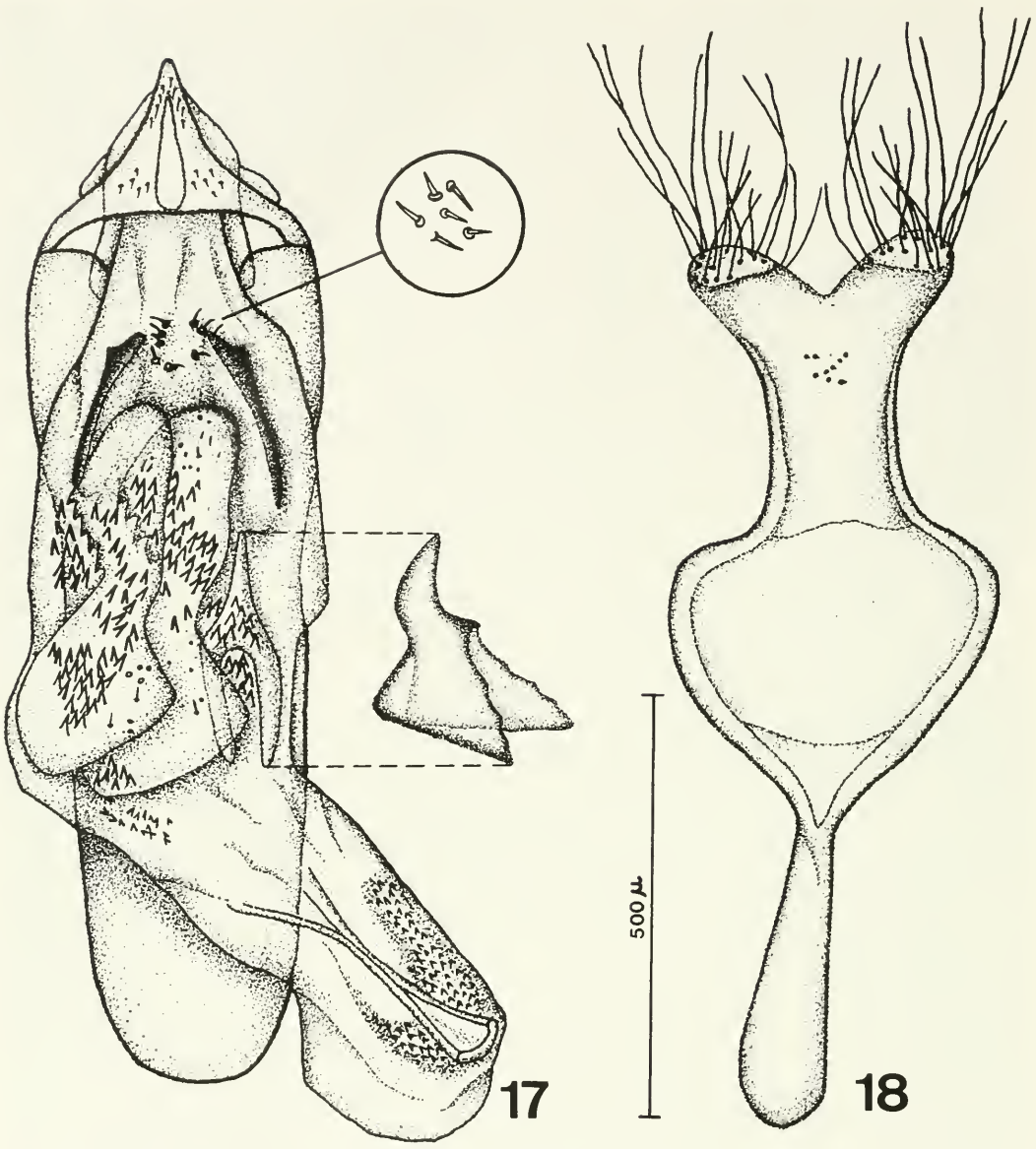


Figs. 9–10. *Amblycerus atypicus*. 9, Scanning electron micrograph (SEM) of the external margin of elytron showing "file." 10, SEM of the inner distal portion of the hind femur showing "scraper."



Figs. 11–16. *Amblycerus ischiodontus*. 11, Dorsal habitus. 12, Scutellum. 13, Metepisternum. 14, Hind leg. 15, Ventral margin of hind femur showing the tooth. 16, Antenna.

of it (Fig. 13). Hind coxa with coarse punctures slightly denser in distal half. Hind femur (Fig. 14) 2.3 times as long as wide and with tooth pronounced in distal portion of ventral margin (Fig. 15); internal face on distal region without transverse striations. Hind tibia (Fig. 14) with coronal denticles approximately of same size; lateral spur 2.4 times length of median, first hind tarsal segment 1.2 times as long as lateral spur and



Figs. 17–18. *Amblycerus ischiodontus*. 17, Male terminalia, median lobe. 18, Same, tegmen and lateral lobes.

2.8 times median spur; ventral face moderately convex with inconspicuous lines of punctures and setae in margins. Male pygidium vertical, round apically. Fifth visible abdominal sternum not emarginate in male. Female unknown.

Male terminalia (Figs. 17, 18): Eighth tergite rounded apically. Median lobe (Fig. 17) with length 3.8 times its largest width in basal area; ventral valve moderately long, acute apically, with concave lateral margins; dorsal valve subtriangular with straight lateral margins and rounded apex. Basal area (Fig. 17) of internal sac without anterior and median sclerites; a pair of posterior thin sclerites, prolonged and with a tooth sub-basally on one side. Median area of internal sac (Fig. 17) with a pair of lam-

inar sclerites, sinuous, serrate sub-basally, teeth approximate; unpaired sclerite in fork form 0.6 times as long as laminars, with moderately separate stems. In apical area of internal sac (Fig. 17) one sclerite with very long stems. Median and apical areas of internal sac with denticles near apical sclerite. Tegmen (Fig. 18) with moderate emargination in "V" between enlarged lateral lobes.

Discussion.—*Amblycerus ischiodontus* shares with *A. eustrophoides, A. pollens,* and *A. stridulator* an area of the metepisternum with transverse striations (Fig. 13) and an apical tooth on the ventral margin of the metafemur (Fig. 15). The study of all characters together did not show great affinity among the mentioned species. Differences are easily recognized in the patterns of pubescence, form of the striate area, and the sclerites in the male internal sac.

Kingsolver et al. (1993) commented that *A. pollens* is more similar to *A. eustrophoides* when compared with *A. stridulator.* Romero et al. (1996) included *A. eustrophoides* in the *alternatus* group along with *A. serieguttatus, A. alternatus,* and *A. schwarzi* and stablished the *stridulator* group only for *A. stridulator.*

Revisionary studies on Brazilian species under way indicate that *A. pollens* and *A. ischiodontus* are members of two distinct species groups, respectively.

According to Arrow (1904) the body area where the stridulatory mechanism is placed in Coleoptera can be the same in non-related groups, as it can be different in different members of the same group. According to him, there are Coleoptera with the two types of stridulatory mechanism placed in different parts of the body.

Amblycerus ischiodontus is easily separated from all other *Amblycerus* by its characteristic form and disposition of sclerites in the male internal sac (Fig. 17).

Type.—Holotype ♂. BRAZIL: Amazonas, Paraná do Xiboreninho, 03°15′S–06°00′W; 5 Aug. 79; mixed water; Canopy Fogging Project TRS#05, Tray 326 Adis, Erwin, Montgomery et al. collectors; deposited in the National Museum Natural of History, Smithsonian Institution, Washington, D.C., U.S.A.

Etymology.—The name of the species refers to the presence of a tooth on the ventral margin of the hind femur.

Key to *Amblycerus* Species with Areas of Integument Probably Involved in Stridulation

1. External margins of elytra partly with an area with overlapping scales (Figs. 3, 9); inner distal portion of hind femur with fine transverse striation (Figs. 6, 10); usually scattered black spots on elytra (Fig. 1); pygidium with large, ovate, velvety dark brown spot (Fig. 4) 2
– Elytra and hind femur without integumental modifications; patterns of coloration on elytra and pygidium otherwise 7
2. Elytra with white hairs vaguely mottled; very coarse punctures on lateral third of pronotum; male terminalia with four pairs of sclerites and one unpaired sclerite . . . . . *Amblycerus guazumicola* (Kingsolver and Johnson)
– Elytra usually with well marked white irregular spots on median and external margins and small irregular patches on remainder of elytra (Fig. 1); moderately coarse punctures on lateral third of pronotum; number of sclerites in internal sac of male terminalia otherwise 3
3. Male internal sac with three pairs of sclerites and one unpaired sclerite (Fig. 7) . . . . . *Amblycerus atypicus,* new species
– Male internal sac with two pairs of sclerites and one unpaired sclerite 4
4. Pair of laminar sclerites in male internal sac with tooth 5
– Pair of laminar sclerites in male internal sac smooth . . . . . *Amblycerus whiteheadi* Kingsolver
5. Male internal sac with basal pair of sclerite spine-shaped 6
– Male internal sac with basal pair of sclerite Y-shaped . . . . . *Amblycerus cistelinus* (Gyllenhal)
6. Male internal sac with unpaired median sclerite serrate basally along one side . . . . . *Amblycerus sosia* Ribeiro-Costa and Kingsolver
– Male internal sac with unpaired median sclerite with serration only on base . . . . . *Amblycerus jatayensis* (Pic)
7. Metepisternum with striate area transverse to metepisternal sulcus, apparently being a modification of metepisternum; apical portion of ventral margin of metafemur finely striate, with conspicuous tooth; pygidium with median line

. . . *Amblycerus stridulator* Kingsolver, Romero N., and Johnson

– Metepisternum with striate area running with longitudinal axis of metepisternal sulcus, apparently being a modification of it; apical portion of ventral margin of metafemur with conspicuous or inconspicuous smooth tooth; pygidium with or without median line 8

8. Apical portion of ventral margin of metafemur with one inconspicuous tooth; posterior end of metepisternum straight on striate area . . . . . *Amblycerus pollens* (Sharp)

– Apical portion of ventral margin of metafemur with one conspicuous tooth; posterior end of metepisternum curved on striate area 9

9. Posterior end of metepisternum gently curved on striate area; scutellum tridentate; pygidium with narrow median line . . . . . *Amblycerus eustrophoides* (Schaeffer)

– Posterior end of metepisternum strongly curved on striate area (Fig. 13); scutellum tridentate on round base (Fig. 12); pygidium otherwise . . . *Amblycerus ischiodontus*, new species

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A REVIEW OF THE BEACH-FLY GENUS *ISOCANACE* MATHIS (DIPTERA: CANACIDAE)

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Abstract.—The species of the beach-fly genus *Isocanace* Mathis are reviewed, including the description of two new species: ***I. crosbyi*** (New Zealand. South Island. NN: Cable Bay (41°09.6′S, 173°24.9′E) and ***I. freidbergi*** (Kenya. Takaungu (50 km N of Mombasa)). Descriptions for the genus and two species groups are also revised.

Key Words: review, Diptera, Canacidae, beach flies, *Isocanace, I. crosbyi, I. freidbergi,* Old World

Recent field work on New Zealand has led to the discovery of the first species of the beach-fly family Canacidae from that country and has also prompted the research that resulted in this review of the genus *Isocanace* Mathis. *Macrocanace* Tonnoir and Malloch, with two endemic species from New Zealand, had previously been included in the Canacidae (Harrison 1959), but is now assigned to the family Tethinidae (Mathis and Munari 1996).

The New Zealand species of Canacidae is undescribed and is in the genus *Isocanace* where it is the second known species of the *Isocanace albiceps* group. The first species of that group, *I. albiceps* (Malloch), is from Australia (Mathis 1996). The new species is apparently widespread on New Zealand, occurring on both North and South Islands and undoubtedly on some of the associated offshore islands.

I am also taking this opportunity to describe an Afrotropical species of *Isocanace* that Amnon Freidberg and Fini Kaplan collected some years ago in Kenya. The latter species belongs to the *Isocanace briani* group, which previously comprised three Afrotropical species: *I. australis* Mathis (Kenya, South Africa), *I. briani* Mathis (Aldabra, Madagascar), and *I. flava* (Canzoneri and Meneghini; Zaire). The last species, *I. flava,* is unusual among beach flies, being one of just a few canacid species that occurs in freshwater habitats. As implied by the common name for the family, most species occur in saline habitats, especially along maritime coasts. The new species from Kenya is very similar to and is apparently the sister species of *I. flava,* although it is found in saline environments along the western coast of the Indian Ocean.

The addition of two new species to *Isocanace,* one to each of the species groups, alters the generic and species-group characterizations, which are revised. A revised key to the species groups and species is also provided.

Isocanace is a relatively recent genus in the nomenclatural history of the Canacidae (Mathis 1982), and the genus has been treated in only two subsequent papers (Mathis 1992, 1996). The first paper is a world catalog, and the second is a review of the Australian beach flies. *Isocanace* is known only from the Afrotropical and Australasian Regions of the Old World (Mathis

1992). This apparently disjunct distribution is probably an artifact due to the poor sampling of Canacidae from countries between Australia and Africa rather than the actual distribution of the genus. Nothing is known about the immature stages or most other aspects about the biology of the included species except for brief comments on habitats where specimens have been collected.

The descriptive format for the new species follows Mathis and Wirth (1979) and Mathis (1982, 1988). More details concerning the morphology and higher classification of the Canacidae are found in Mathis (1982, 1992) and Wirth (1987). I follow Crosby et al.'s (1976) geographic codes for New Zealand zoogeographic provinces: AK = Auckland, NC = North Canterbury, NN = Nelson.

Two venational ratios are used in the descriptions. Costal vein ratio: The straight line distance between the apices of vein R_{2+3} and R_{4+5}/distance between the apices of veins R_1 and R_{2+3}. M vein ratio: The straight line distance along vein M between crossveins (r-m and dm-cu)/distance apicad of dm-cu.

Specimens are housed in the following institutions (acronyms are used in the descriptive portion of this paper).

AM Australian Museum, Sydney, Australia

ANIC The Australian National Insect Collection, Division of Entomology, CSIRO, Canberra, Australia

MNHN Muséum National d'Histoire Naturelle, Paris, France

MRAC Musée Royal de l'Afrique Centrale (Koninklijk Museum voor Midden-Afrika), Tervuren, Belgium

NMP Natal Museum, Pietermaritzburg, South Africa

NZAC New Zealand Arthropod Collection, Entomology Division, Landcare Research, Auckland, New Zealand

TAU Tel Aviv University, Tel Aviv, Israel

UQIC University of Queensland Insect Collection, Brisbane, Australia

USNM former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

Genus *Isocanace* Mathis

Isocanace Mathis 1982: 11. Type species: *Isocanace briani* Mathis, by original designation.—Mathis 1992: 5–6 [world catalog]; 1996: 337–339 [Australian fauna].

Canace, in part, of authors: Mathis and Wirth 1979: 786.

Diagnosis.—Resembling *Chaetocanace* Hendel but differing from it and other genera by the following combination of characters.

Head: Mesofrons distinct from parafrons, shinier, less microtomentose, with 2–3 large, lateral, generally proclinate setae; postocellar seta smaller than ocellar seta and with more proclinate orientation; 3–4 pairs of large, lateroclinate, fronto-orbital setae; arista plumose, length of branched rays varying from approximately subequal to nearly twice basal aristal width; dorsally genal setae 2–3; dorsally curved genal seta 1.

Thorax: Dorsocentral setae 4 (1+3); acrostichal setae evident, in 2 rows, but large, prescutellar pair lacking; 2 pairs of scutellar setae and frequently some smaller setae inserted dorsally; with only 1 supra-alar seta; 1–2 notopleural setae, if only 1, anterior seta lacking; color of pleural setae variable, pale yellow to black; postpronotum bare of setulae; katepisternal seta present or absent; 1 large anepisternal seta; hindtibia lacking apical seta anteroventrally; apical section of vein M straight.

Abdomen: Female genital lamellae very broad basally, basilateral margins rounded, narrowed rather abruptly at level of cleft, lamellae very narrow from level of cleft to apices, with only 1 large, stout, acute terminal seta at each apex. Male surstylus

quite variable, generally slender and with apical curvature.

Distribution.—Old World. Afrotropical (Aldabra, Kenya, Madagascar, South Africa, and Zaire), Australian (New South Wales), New Zealand.

Discussion.—Mathis and Wirth (1979) first noted the possible relationship of some species subsequently placed in *Isocanace* in the remarks section of *Canace stuckenbergi* (=*I. briani*). Mathis (1982) concluded that this group of species is a monophyletic lineage that is more closely related to *Chaetocanace* than to *Canace* Haliday, sensu stricto, and named it as the genus *Isocanace*. Study of the type series of *Canace flava* Canzoneri and Meneghini revealed that this species too is closely related to *I. briani*, thus making a total of four described species. The addition of two new species brings the number of described species to six.

Key to Species Groups and Species of *Isocanace*

1. Katepisternal seta lacking; mesofrons bare in middle; anterior notopleural seta subequal to posterior seta; 2 dorsally genal setae (Australasian, the *Isocanace albiceps* group) 2
– Katepisternal seta present, although sometimes pale; mesofrons with scattered setulae on middle; anterior notopleural seta distinctly smaller than posterior seta or lacking; 3 dorsally genal setae (Afrotropical, the *Isocanace briani* group) 3
2. Specimens generally more tan to brown, especially frons, and somewhat on mesonotum and dorsum of abdomen; acrostichal setulae sparse and in 2 rows; scutellum conspicuously wider than long; surstylus narrow, apex with recurved knob (Australia) . . . *I. albiceps* (Malloch)
– Specimens generally gray, frons appearing bluish to blackish gray, mesonotum and dorsum of abdomen whitish gray to gray, at most partially tannish medially; acrostichal setulae comparatively numerous and in 4 rows, lateral row with fewer setulae; scutellum almost as long as wide; surstylus broad, apex not recurved or knoblike (New Zealand) . . . . . *I. crosbyi*, new species
3. Arista with branching rays long, some nearly double aristal width at base; anepisternal and usually katepisternal seta pale, mostly yellowish (Madagascar and Aldabra Islands) . . . . . *I. briani* Mathis
– Arista with branching rays shorter, at most slightly longer than aristal width at base; anepisternal and katepisternal seta black 4
4. Anterior notopleural seta present, although weaker than posterior seta; surstylus in lateral view narrow, with subapical posterior swelling bearing several pale setae, apical ⅓ curved posteriorly (Kenya, South Africa) . . . . . *I. australis* Mathis
– Anterior notopleural seta lacking or very weak and pale; surstylus wider in lateral view, with subapical anterior swelling, apical ⅓ narrowed considerably and curved anteriorly 5
5. Lateroclinate fronto-orbital setae 4. Compressed sickle-shaped portion of surstylus narrow (Fig. 29) (Zaire) . . . . . *I. flava* (Canzoneri and Meneghini)
– Lateroclinate fronto-orbital setae 3. Compressed sickle-shaped portion of surstylus broad (Fig. 30) (Kenya) . . . . . *I. freidbergi*, new species

Isocanace albiceps Group

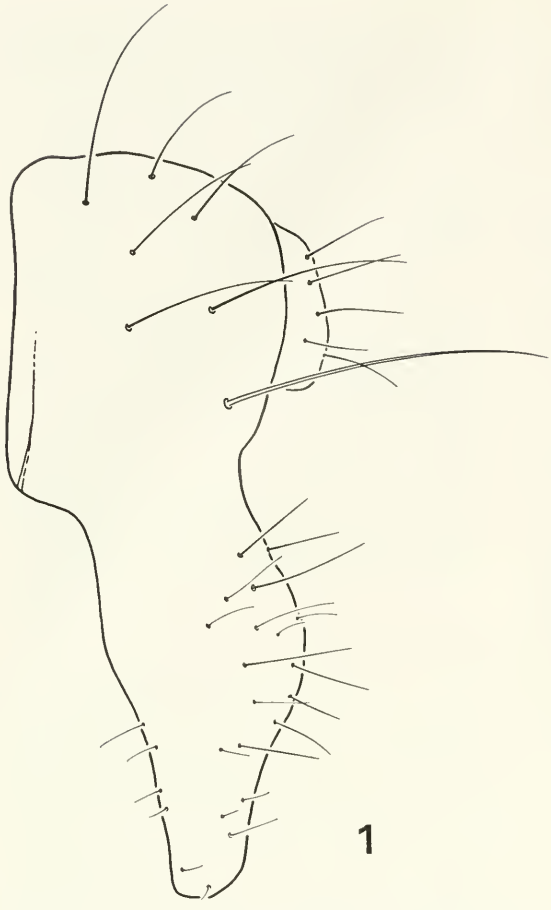
Diagnosis.—Differing from the *Isocanace briani* group as follows: *Head:* mesofrons bare in middle; lateroclinate fronto-orbital setae 4; dorsally genal setae 2. *Thorax:* anterior notopleural seta subequal to posterior seta; katepisternal seta lacking; femora concolorous, usually gray to brownish gray.

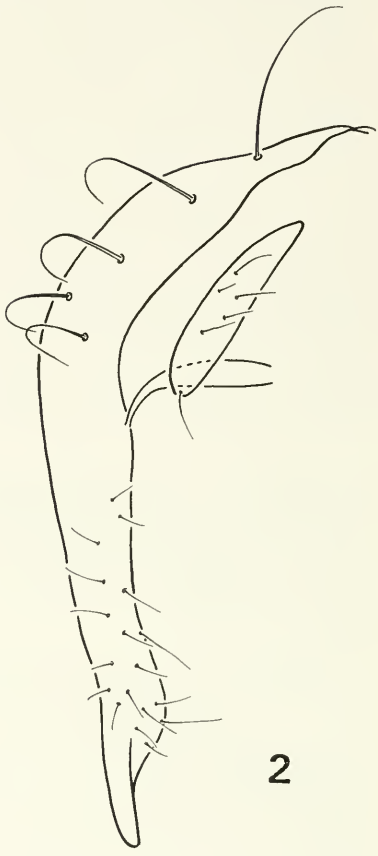
Distribution.—Australasian: Australia, New Zealand.

Isocanace crosbyi Mathis, new species
(Figs. 1–2)

Description.—This species is similar to *I. albiceps* but is distinguished from it and other congeners by the following combination of characters: small to moderately-small beach flies, length 1.55–2.15 mm.

Head: Mesofrons whitish gray to bluish gray, subshiny, lacking setulae in middle; lateroclinate fronto-orbital setae 4. Antenna black with sparse, whitish gray microtomentum; arista bearing short branching hairs, these not much longer than basal aristal width. Gena with 2 large dorsally setae and only 2 setulae anterior of ventral dor-





Figs. 1–2. External male terminalia of *Isocanace crosbyi*. 1, Epandrium, cercus, and surstylus, lateral view. 2, Surstylus, posterior view.

sally seta, rarely with a posterior setula. Maxillary palpus yellow.

Thorax: Mesonotum brownish gray to bluish gray to gray, varying from somewhat contrasted to concolorous with grayish pleural region; acrostichal setulae in 4 rows, lateral row somewhat irregular and with fewer setulae; anterior notopleural seta well developed, subequal in size and color to posterior seta; scutellum almost as long as wide. Wing: costal vein ratio 0.15–0.18; M vein ratio 0.38–0.45; crossvein r-m slightly but consistently basad of middle of discal cell. Femora and tibiae gray, concolorous with pleural region; tarsi yellow.

Abdomen: Male terminalia (Figs. 1–2): Surstylus in lateral view (Fig. 1) as high as epandrium, wider medially, tapered thereafter to broadly rounded ventral apex; in posterior view (Fig. 2) surstylus tapered very slightly toward venter until apical ¼ where medial margin tapered more abruptly, making apex narrow and parallel sided.

Type Material.—The holotype ♂ is labeled "NEW ZEALAND. S[OUTH] ISL[AND]. NN: Cable Bay (41°09.6′S, 173°24.9′E), 13 Feb 1998 [,] Wayne N. Mathis." The holotype is double mounted (minuten in a block of plastic), is in excellent condition, and is deposited in NZAC. Twenty-seven paratypes (24 ♂, 3 ♀; NZAC, USNM) bear the same label data as

the holotype. Other paratypes are as follows: NEW ZEALAND. North Island: AK: Auckland Centennial Park (37°0.7′S, 174°36.3′E), 18 Feb 1998, W. N. Mathis (3 ♂, 4 ♀; USNM); Taramaire Beach (37°09.1′S, 175°18.5′E), 8 Feb 1998, W. N. Mathis (1 ♂; USNM). ND: Whananaki South (beach; 35°31.1′S, 174°27.2′E), 19 Feb 1998, W. N. Mathis (19 ♂, 10 ♀; NZAC, USNM)

Distribution.—Australasian: New Zealand (AK, NC, NN).

Etymology.—The species epithet is a genitive patronym to recognize the generous assistance of Dr. Trevor K. Crosby (NZAC) to my research on the shore and beach flies of New Zealand.

Remarks.—There is considerable variability in the color of the dorsal surface, especially the mesonotum. In the series from the type locality, the coloration is mostly bluish gray to gray with just faint tannish to brownish areas medially. But in the long series from Whananaki South there is notably more brownish coloration dorsally. The mesofrons, however, remains mostly silvery to bluish gray in specimens from all localities.

Isocanace albiceps (Malloch)
(Figs. 3–12)

Canace albiceps Malloch 1925: 87 [HT ♀ (AM); Australia. New South Wales: Sydney].—Wirth 1951: 262 [review].

Isocanace albiceps: Mathis 1982: 18 [generic combination]; 1989a: 670 [Australasian/Oceanian catalog]; 1992: 6 [world catalog]; 1996: 338–339 [Australian fauna].—Colless and McAlpine 1991: 779 [fig. of head].

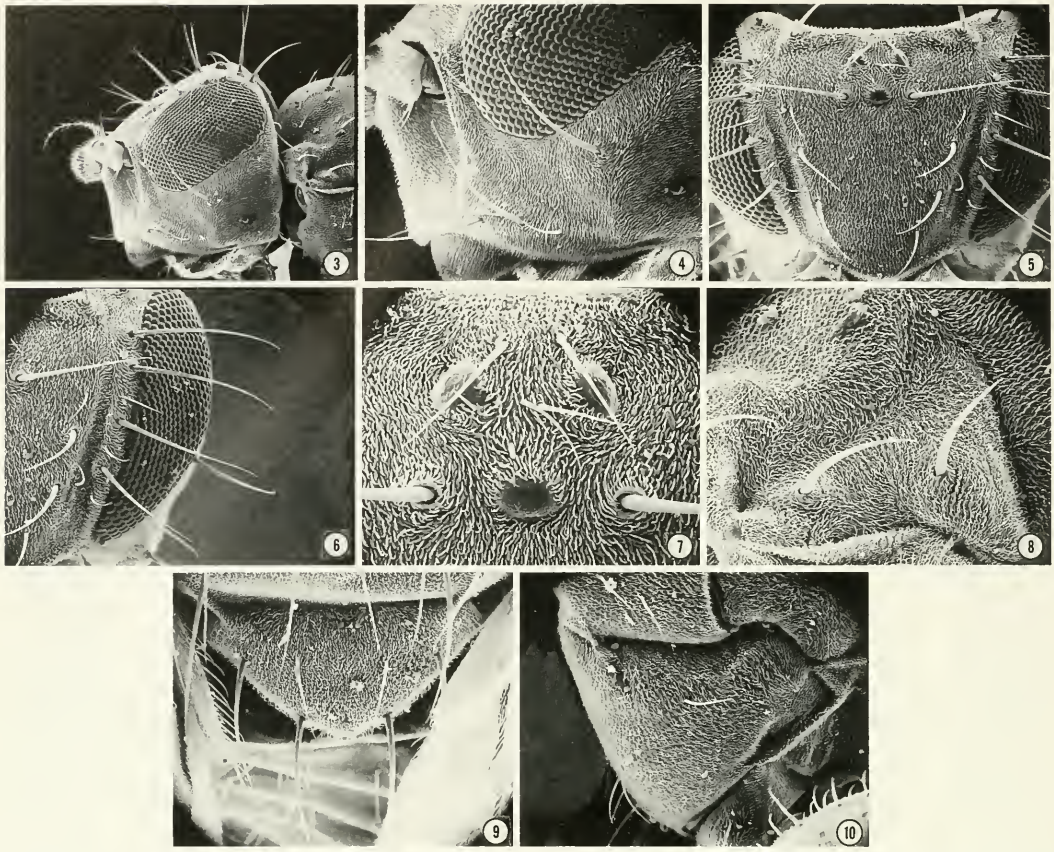
Diagnosis.—Specimens of *I. albiceps* are similar to those of the *Isocanace briani* group and *I. crosbyi* but are distinguished by: mesofrons bare in middle (Fig. 5); postocellar seta short and with more proclinate orientation (Fig. 7); lateroclinate fronto-orbital setae 4; arista with branching rays long, some nearly double basal aristal width (Fig. 3); dorsally curved genal setae 2 (Fig. 4); acrostichal setulae in 2 rows; anterior notopleural seta subequal in length to posterior seta (Fig. 8); anepisternal setae pale; katepisternum lacking a large seta (Fig. 10); crossvein r-m at about middle of discal cell; surstylus (Figs. 11–12) relatively wide in lateral view, narrowed subapically, but slightly widened again apically and slightly bulbous, with slight median projected process; posterior margin of surstylus sinuous, anterior margin straight.

Specimens examined.—AUSTRALIA. New South Wales: Broulee, 17 Sep 1978, Z. Liepa (2 ♂, 3 ♀; ANIC). Careel Bay, 22 Mar–23 Oct 1956, 1962, D. K. McAlpine, W. W. Wirth (35 ♂, 56 ♀; AM, ANIC, USNM). Cornulla (34°2.1′S, 151°9.1′E), 22 Feb 1998, W. N. Mathis (1 ♂, 2 ♀; USNM). Karuah (inlet, beach), 23 Dec 1968, I. C. Yeo (4 ♂, 9 ♀; UQIC). McCarrs Creek, 20 Sep 1956, W. W. Wirth (2 ♂; USNM). Merimbula (mangrove flat), 12 Feb 1963, D. K. McAlpine (1 ♀; AM). Mona Vale, 11 Nov 1956, W. W. Wirth (1 ♂; USNM). North Cronulla (mangroves), 29 Jan–22 Mar 1962, D. K. McAlpine (4 ♂, 3 ♀; AM). Putty Beach (near Terrigal), 25 Nov 1987, R. Blanche, B. Day, D. K. McAlpine (1 ♂; AM). Queensland: Deception Bay, 23 May 1966, Z. Liepa (1 ♂; ANIC). Tasmania. Squeaking Point, near Port Sorell (stony beach), 24 Nov 1968, I. C. Yeo (1 ♂, 8 ♀; UQIC).

Distribution.—Australasian: Eastern Australia (NSW, QLD, TAS).

Isocanace briani Group

Diagnosis.—Differing from the *Isocanace albiceps* group as follows: *Head:* mesofrons with scattered setulae on middle; lateroclinate fronto-orbital setae 3–4; 3 dorsally curved genal setae. *Thorax:* acrostichal setulae in 4 rows, lateral row sometimes with fewer setulae and somewhat irregular; anterior notopleural seta distinctly smaller than posterior seta or lacking; katepisternal seta present, although



Figs. 3–10. Scanning electron micrographs of *Isocanace albiceps*. 3, Head, lateral view. 4, Gena and setae, lateral view. 5, Frons, dorsal view. 6, Same, left side, dorsal view. 7, Ocellar triangle, dorsal view. 8, Notopleuron and setae, lateral view. 9, Scutellum, dorsal view. 10, Katepisternum and setae, lateral view.

sometimes pale; midfemur yellow, contrasted with gray to tan fore- and hindfemur.

Discussion.—The shape and armature of the surstylus in males of the *Isocanace briani* group differ markedly from the generalized condition found in the *Isocanace albiceps* group. At the species level these features appear to be excellent discriminating characters.

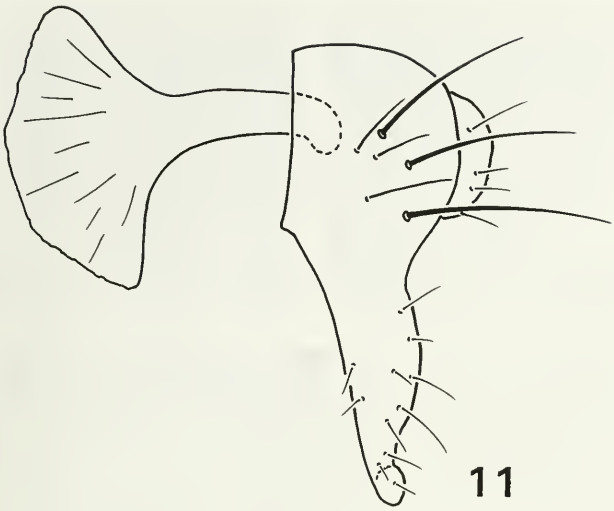
Distribution.—Afrotropical (Aldabra, Kenya, Madagascar, South Africa, Zaire).

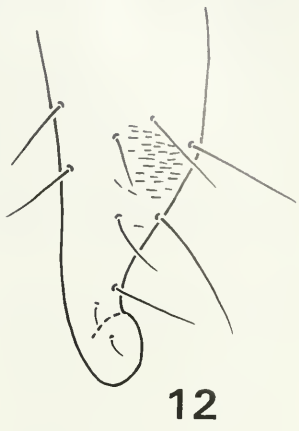
Isocanace australis Mathis
(Figs. 13–14)

Isocanace australis Mathis 1982: 14 [HT ♂ (NMP); South Africa. Cape: Port St. Johns; figure of head and ♂ terminalia]; 1992: 6 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: mesofrons with scattered setulae on middle; lateroclinate fronto-orbital setae 4 (Fig. 13); arista with branching rays shorter, at most slightly longer than aristal width at base; 3 dorsally curved genal setae; anterior notopleural seta distinctly smaller than posterior seta or lacking; anepisternal and katepisternal seta present, black; male terminalia as in Fig. 14.

Specimens examined.—KENYA. Mombasa (100 km N), 4 Dec 1989, A. Freidberg, F. Kaplan (19 ♂, 15 ♀; USNM). Ngomeni (150 km N Mombasa), 4 Dec 1989, A. Freidberg, F. Kaplan (2 ♀; USNM). Takaungu (50 km N Mombasa), 3 Dec 1989, A. Freidberg, F. Kaplan (2 ♀; USNM).





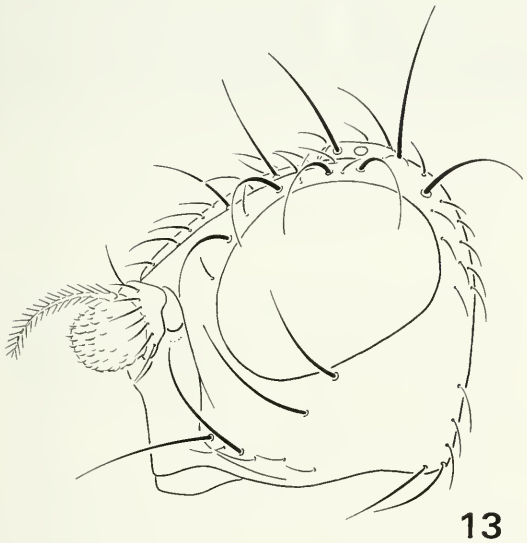
Figs. 11–12. External male terminalia of *Isocanace albiceps*. 11, Epandrium, cercus, and surstylus, lateral view. 12, Surstylus, lateral view.

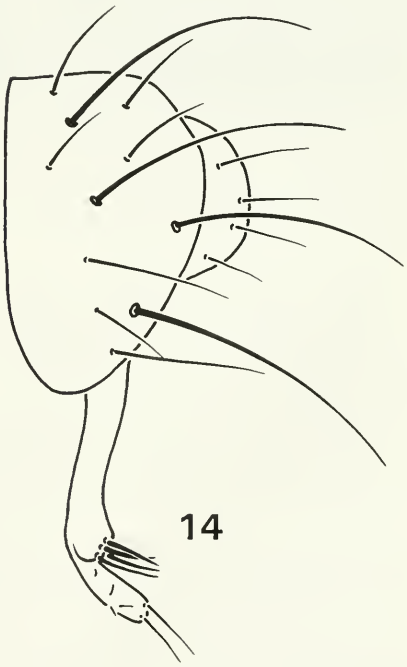
SOUTH AFRICA. Cape Province: Port St. Johns, B. and P. Stuckenberg (2 ♂, 2 ♀; paratypes; USNM).

Distribution.—Afrotropical: Kenya, South Africa (Cape).

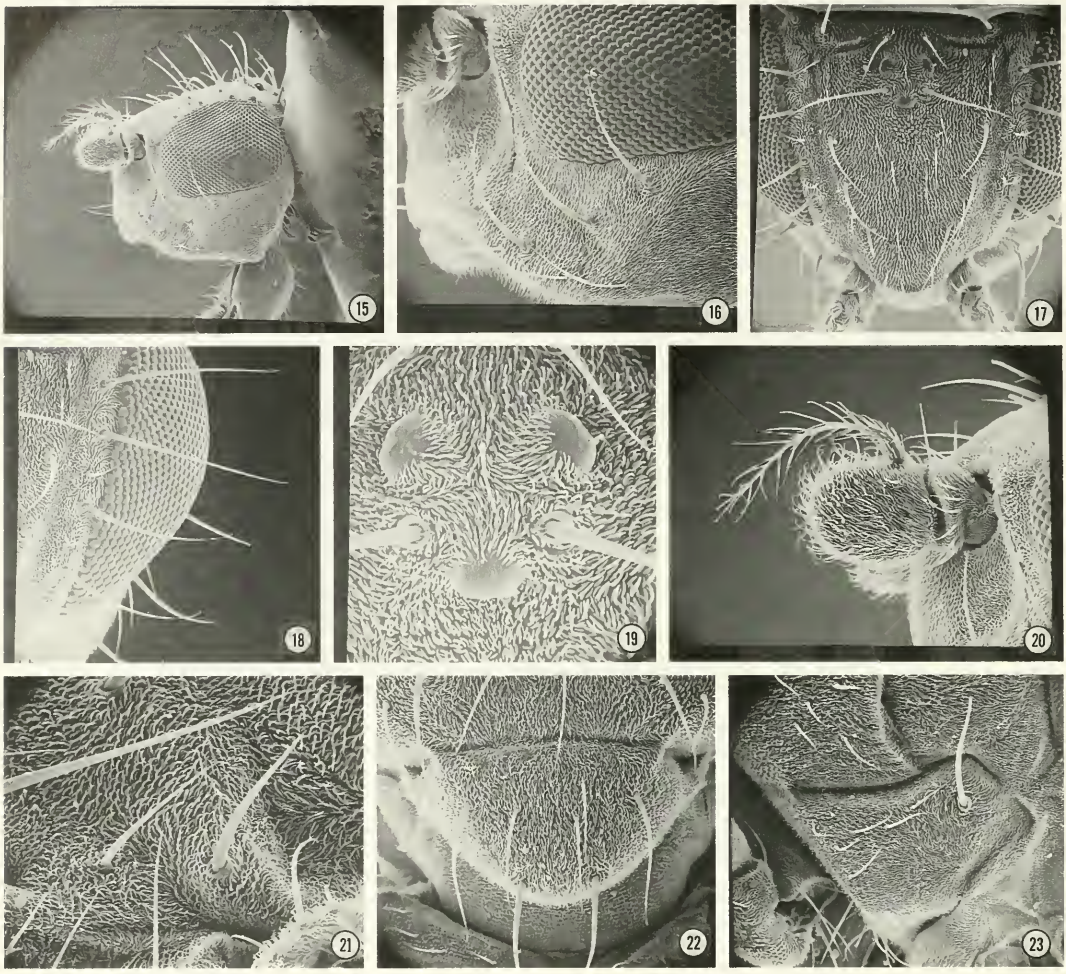
Isocanace briani Mathis
(Figs. 15–25)

Canace stuckenbergi Mathis and Wirth 1979: 786 [HT ♂ (MNHN); Madagascar.





Figs. 13–14. *Isocanace australis*. 13, Head, lateral view. 14, Epandrium, cercus, and surstylus, lateral view.



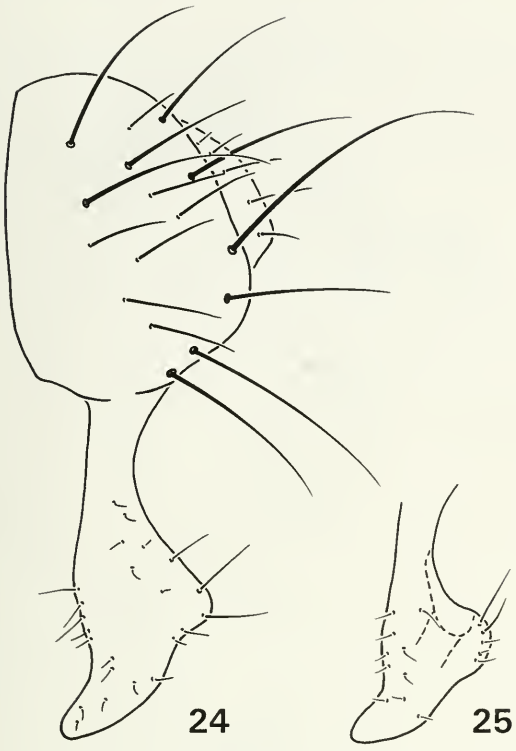
Figs. 15–23. Scanning electron micrographs of *Isocanace briani*. 15, Head, lateral view. 16, Gena and setae, lateral view. 17, Frons, dorsal view. 18, Same, left side, dorsal view. 19, Ocellar triangle, dorsal view. 20, Antenna, lateral view. 21, Notopleuron and setae, lateral view. 22, Scutellum, dorsal view. 23, Katepisternum and setae, lateral view.

Antseranana: Sambirano Lokobe Nosy Bé figure of ♂ terminalia; junior primary homonym, see Wirth 1956: 50].

Isocanace briani Mathis 1982: 15 [new name for *C. stuckenbergi* Mathis and Wirth 1979; figures of head, thorax, and ♂ terminalia]; 1992: 6 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: mesofrons with scattered setulae on middle; lateroclinate fronto-orbital setae 4; 3 dorsally curved genal setae; arista with branching rays long, some nearly double aristal width at base; anterior notopleural seta distinctly smaller than posterior seta or lacking; anepisternal seta pale, mostly yellowish; katepisternal seta present, pale, mostly yellowish.

Specimens examined.—ALDABRA. Grande Terre: Anse Mais, 17 Mar 1986, W. N. Mathis (1 ♂; USNM); Cinq Cases (on mud around saline pools), 23–29 Jan 1968, B. Cogan, A. Hutson (1 ♀; USNM); Point Hodoul (tidal saline pool), 27 Jan 1968, B. Cogan, A. Hutson (1 ♂, 2 ♀; USNM). Malabar: East Channel (near), 18–23 Feb 1968,



Figs. 24–25. External male terminalia of *Isocanace briani*. 24, Epandrium, cercus, and surstylus, lateral view (type locality). 25, Same (Aldabra), lateral view.

B. Cogan, A. Hutson (1 ♂, 1 ♀; USNM). Picard: Bassin Labine (trail to), 20 Mar 1986, W. N. Mathis (12 ♂, 7 ♀; USNM); La Gigi, 19–24 Mar 1986, W. N. Mathis (7 ♂, 20 ♀; USNM); Settlement, 15–21 Mar 1986, W. N. Mathis (3 ♂, 1 ♀; USNM). MADAGASCAR. Antsiranana: Nosy Be, Ambatoloaka (beach), 4–7 Apr 1991, A. Freidberg, F. Kaplan (15 ♂, 25 ♀; USNM). Nosy Be, Andoany (Hell-Ville), 5 Apr 1991, A. Freidberg, F. Kaplan (4 ♂, 2 ♀; USNM). Nosy Be, Sambirano, Lokobe (6 m; rocks on beach), 9–23 Nov 1957, B. Stuckenberg (4 ♂, 13 ♀; USNM). Ramena, 10 Apr 1991, A. Freidberg, F. Kaplan (2 ♂, 18 ♀; USNM). Nosy Domba, 6 Apr 1991, A Freidberg, F. Kaplan (1 ♀; USNM).

Distribution.—Afrotropical: Madagascar (Antsiranana), Seychelles (Aldabra).

Isocanace flava (Canzoneri and Meneghini)
(Figs. 26–29)

Canace flava Canzoneri and Meneghini 1969: 184 [HT ♂ (MRAC); Zaire. Albert National Park: May ya Moto].—Cogan 1980: 694 [Afrotropical catalog].

Isocanace flava: Mathis 1982: 17 [generic combination; figures of head, thorax, ♂ terminalia]; 1992: 6 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: mesofrons with scattered setulae on middle (Fig. 26); lateroclinate fronto-orbital setae 4 (Figs. 26–27); arista with branching rays shorter, at most slightly longer than aristal width at base (Fig. 27); 3 dorsally curved genal setae (Fig. 27); anterior notopleural seta distinctly smaller than posterior seta or lacking; anepisternal and katepisternal seta present, black; male terminalia as in Fig. 29.

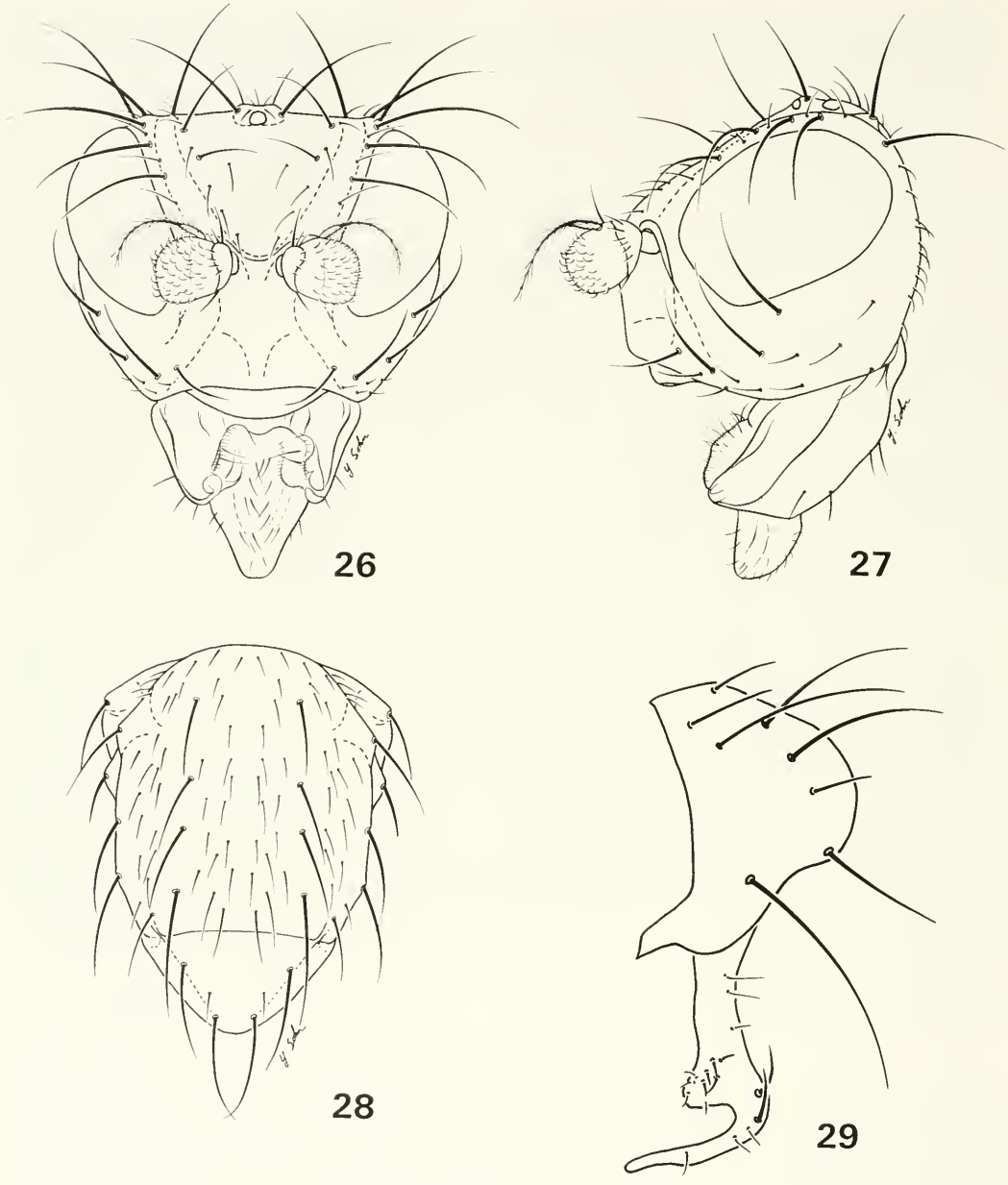
Distribution.—Afrotropical: Zaire (Haut-Zaire).

***Isocanace freidbergi* Mathis, new species**
(Figs. 30–31)

Description.—This species is similar to *I. flava* but is distinguished from it and other congeners by the following combination of characters: small to moderately-small beach flies, length 1.65–2.40 mm; mostly gray.

Head: Mesofrons whitish gray to tannish gray, bearing scattered setulae on middle and 2–3 large, lateral proclinate setae; lateroclinate fronto-orbital setae 3. Antenna mostly yellow but with varying amounts of blackish overlay, especially on flagellomere 1; arista bearing short branching hairs, these at most slightly longer than aristal width at base. Large, dorsally curved genal setae 3, 1 large anteroclinate seta, and 3–5 much smaller, anteroclinate setulae.

Thorax: Acrostichal setulae in 4 somewhat irregular rows of numerous setulae and with a larger, prescutellar pair; anterior notopleural seta either lacking or pale and much smaller than posterior seta; anepisternal and

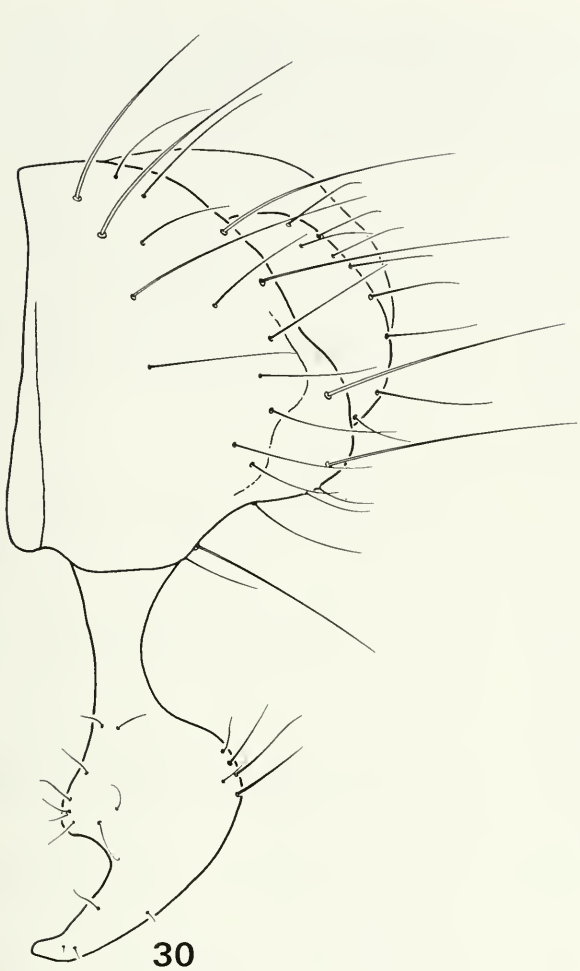


Figs. 26–29. *Isocanace flava.* 26, Head, anterior view. 27. Same, lateral view. 28, Thorax, dorsal view. 29, Epandrium and surstylus, lateral view.

katepisternal seta present, black. Wing with costal vein ratio 0.21; M vein ratio 0.36–0.47. Femora of mid and hindlegs mostly microtomentose, gray, concolorous with pleural region, midfemora more yellowish but with some faint investment of gray microtomentum; tibiae and tarsi yellow.

Abdomen: Male terminalia (Figs. 30–31): Surstylus in lateral view irregularly hooklike to sickle shaped (Fig. 30), widest at basal ⅓, apex pointed, curved anteriorly; in posterior view as in Fig. 31.

Type Material.—The holotype ♂ is labeled "KENYA Takaungu, 50 km North



Figs. 30–31. External male terminalia of *Isocanace freidbergi*. 30, Epandrium, cercus, and surstylus, lateral view. 31, Same, posterior view.

Mombasa 3. XII. 1989 A. FREIDBERG & FINI KAPLAN." The holotype is double mounted (minuten in a block of plastic), is in excellent condition, and is deposited in the USNM. Thirty-nine paratypes (14 ♂, 25 ♀; TAU, USNM) bear the same label data as the holotype. Other paratypes are as follows: *KENYA*. Gazi (60 km S Mombasa; route A14), 5 May 1991, A. Freidberg, F. Kaplan (3 ♂, 3 ♀; TAU, USNM).

Distribution.—Afrotropical: Kenya.

Etymology.—The species epithet is a genitive patronym to recognize the importance of the collecting efforts of Dr. Amnon Freidberg (TAU) to my research on the shore and beach flies of Africa.

Remarks.—This species is apparently the sister species of *I. flava*, with supporting evidence being the hook to sicklelike apex of the surstylus in lateral view (Figs. 29, 31). Unlike its sister species, which is found in freshwater habitats in the Rift Valley (eastern Zaire), this species occurs in coastal habitats that are saline.

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TYPES AND BIOLOGICAL NOTES OF THE EASTERN NORTH AMERICAN SAWFLIES OF *PONTANIA* COSTA AND *PHYLLOCOLPA* BENSON (HYMENOPTERA: TENTHREDINIDAE) DESCRIBED BY MARLATT, DYAR, AND ROHWER

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Abstract.—The taxonomic placement of 18 sawfly species assigned to *Pontania* and *Phyllocolpa* or described under *Pontania* from eastern North America by Marlatt, Dyar, and Rohwer are discussed. The authorship of *Pteronus carpini, Pontania consors,* and *P. borealis* attributed to Marlatt is changed to Dyar. The following eight species from eastern North America belong to *Pontania* (*Eupontania*): *P.* (*E.*) *s-desmodioides* (Walsh) (= *Pontania borealis* Dyar 1898, **n. syn.**); *P.* (*E.*) *s-pisum* (Walsh); *P.* (*E.*) *s-pomum* (Walsh); *P.*(*E.*) *gracilis* Marlatt; *P.* (*E.*) *rugulosa* Marlatt; *P.* (*E.*) *petiolaridis* Rohwer; *P.* (*E.*) *consors* Dyar; and *P.* (*E.*) *lucidae* Rohwer. Three species are included in the leaf-rolling *crassispina* group of the subgenus *Pontania*: *P.* (*P.*) *pumila* Rohwer; *P.* (*P.*) *populi* Marlatt; and *P.* (*P.*) *terminalis* Marlatt. Five species are included in the genus *Phyllocolpa: P. nigrita* (Marlatt); *P. pectoralis* (Marlatt); *P. robusta* (Marlatt); *P. leavitti* (Rohwer); and *P. crassicornis* (Rohwer), **n. comb.** *Pontania acuminata* Marlatt is transferred to *Nematus,* **n. comb.** Lectotypes are designated for seven species. The *Salix* and *Populus* host plants are given and associated galls are illustrated.

Key Words: *Pontania, Phyllocolpa,* sawflies, leaf galls, leaf folds, Marlatt, Dyar, Rohwer

The Nearctic gall-making and leaf-folding sawflies have received little attention and have not been revised due to few apparent morphological characters in the adults and lack of information on associated galls, habits, and other biological data. Smith (1979) listed the gall-forming species of Nematinae in the genera *Euura, Pontania,* and *Phyllocolpa,* following the classification in place at that time. Subsequent work on the Palearctic fauna by Vikberg (1982) and Zinovjev (1993), has refined the classification, most notably by the recognition of various subgenera and species groups within each genus. Consequently, the taxa described from the Nearctic Region need to be reevaluated, and associated galls and host information recorded where known.

In this paper, we discuss the species of *Pontania* and *Phyllocolpa* described by Marlatt, Rohwer, and Dyar from eastern North America. The authorship of three species are correctly attributed to Dyar rather than Marlatt. The species described by these authors are significant because many have associated galls, host, and biological information. These authors are also responsible for all of the species of *Phyllocolpa* and half of the species of *Pontania* known

from eastern North America. We use the diagnostic characters and classification used by Zinovjev (1993), except that *Phyllocolpa* is treated as a genus rather than a subgenus of *Pontania*. Following is a summary of the classification and biological information for the subtribe Euurina:

Subtribe Euurina—Produces galls or leaf folds on Salicaceae, mainly *Salix* spp., but a few on *Chosenia* in eastern Asia and on *Populus* in North America.

Genus *Euura* Newman—Produces bud, stem, petiole, or midrib galls.

Genus *Phyllocolpa* Benson—Larvae in rolled leaves or leaf margins, without swelling at site of egg laying. At least two species groups in North America, *leucapsis* and *leucosticta*.

Genus *Pontania* Costa

Subgenus *Pontania* Costa—Larvae in closed galls or leaf rolls, with site of egg laying marked by distinct swelling on upper surface of leaf. Three species groups: *crassispina, dolichura, proxima*.

Subgenus *Eupontania* Zinovjev—Larvae produce closed leaf galls attached to the midvein or occasionally a larger lateral vein. At least two of the five Palearctic species groups occur in North America, *polaris* and *viminalis*.

Five species treated here belong in *Phyllocolpa*, two in the *leucosticta* group, two in the *leucapsis* group, and one is not placed. *Phyllocolpa crassicornis* (Rohwer) was not included in the review by Smith and Fritz (1996). *Pontania acuminata* Marlatt, *P. populi* Marlatt, and *P. terminalis* Marlatt, included in *Phyllocolpa* by Smith and Fritz (1996), are here transferred to *Pontania* or *Nematus*.

The subgenus *Pontania* is represented by three species groups in North America. The gall-making *Pontania proxima* (Lepeletier), which was described under the name *Messa hyalina* by Norton (1864), was introduced from Europe together with the host plants *Salix alba* L., *Salix fragilis* L., and their hybrids, and it is the only representative of the *proxima* group known in temperate North America. Galls of an undescribed species of the *dolichura* group on *Salix sericea* (Marsh.) were found in Otsego Co., N.Y., in July 1996 by A. G. Zinovjev and R. Fritz. Similar galls have been encountered on *S. nigra* Marsh. and other willows in the Harvard University Herbaria by AGZ. We recognize three species of the leaf-rolling *crassispina* group, *P.* (*P.*) *pumila* Rohwer, *P.* (*P.*) *populi* Marlatt, and *P.* (*P.*) *terminalis* Marlatt.

The following eight species from eastern North America belong to *Pontania* (*Eupontania*): *P.* (*E.*) *s-pisum* (Walsh), *P.* (*E.*) *s-pomum* (Walsh), *P.* (*E.*) *s-desmodioides* (Walsh), *P.*(*E.*) *gracilis* (Marlatt), *P.* (*E.*) *rugulosa* Marlatt, *P.* (*E.*) *petiolaridis* Rohwer, *P.* (*E.*) *consors* Dyar, and *P.* (*E.*) *lucidae* Rohwer. Their galls (Figs. 1–9) help distinguish the species. The Walsh species are newly assigned to this group.

For some of the species discussed, the remnants of the galls from which type specimens were reared are still preserved, and we illustrate these. These remnants made it possible to check the host plant identifications by G. Argus. Acronyms used for museums are: USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; CUIC = Cornell University, Ithaca, New York.

Species Described by Marlatt

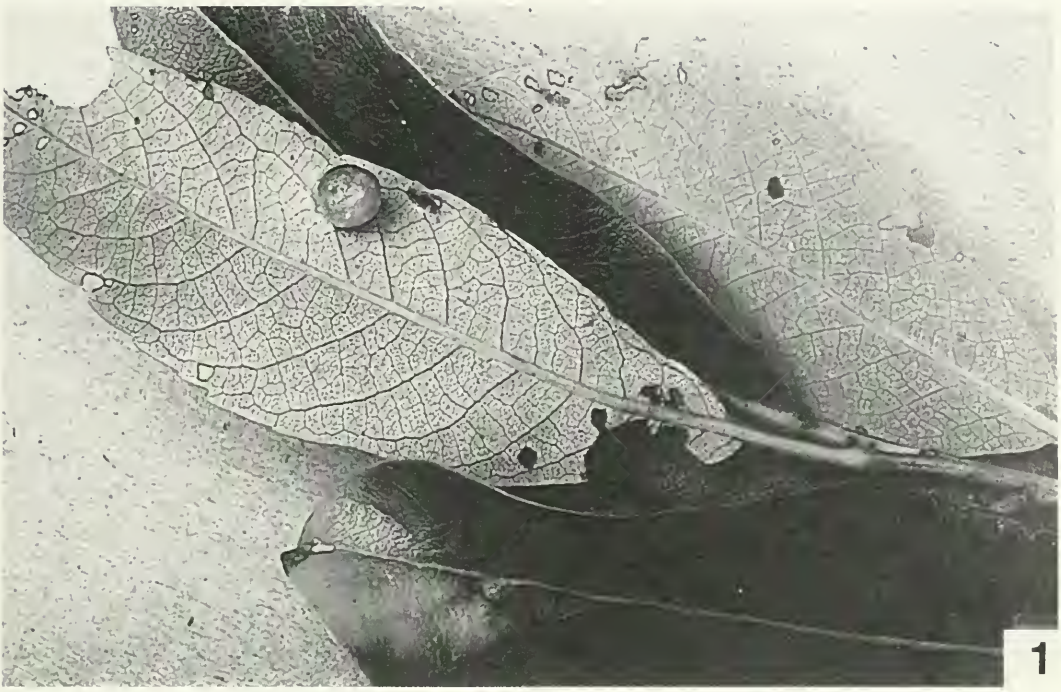
Pontania acuminata Marlatt 1896a: 32.

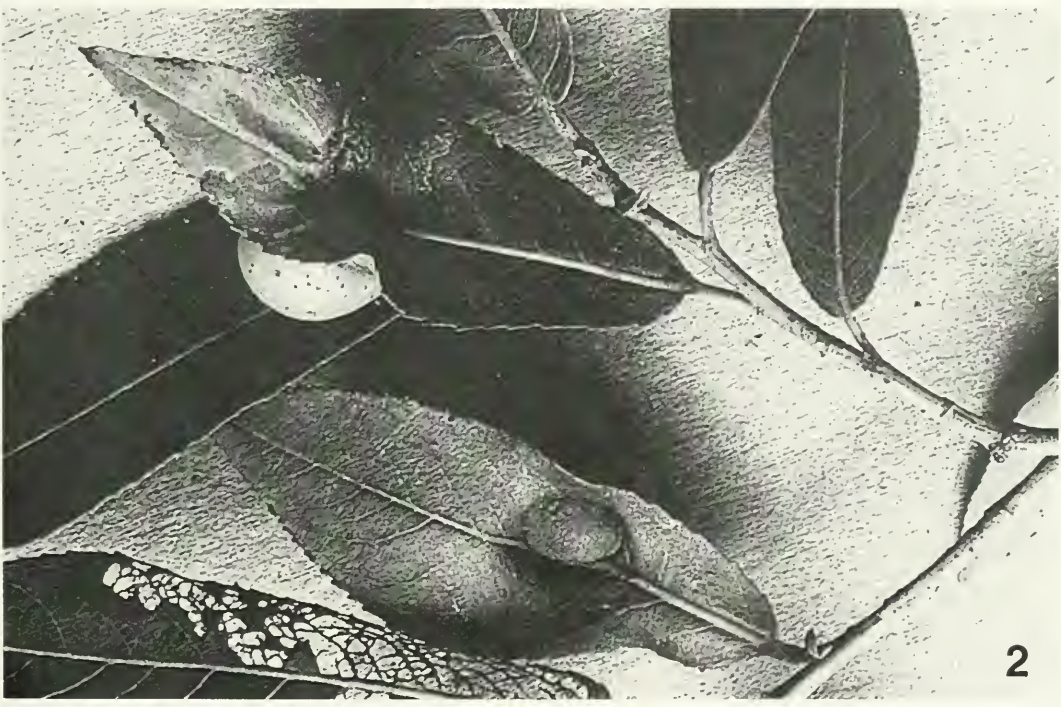
Type locality.—Michigan. The holotype is labeled "Ag.Coll. Mich.," presumably from East Lansing.

Type material.—Described from one female. The holotype was redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host plant.—Unknown.

Notes.—Examination of the ovipositor of





Figs. 1–2. Galls of *Pontania* (*Eupontania*) spp., Milford, Otsego Co., N.Y. 1, *P.* (*E.*) *s-pisum* on *Salix discolor*. 2, *P.* (*E.*) *s-ponum* on *Salix eriocephala*.

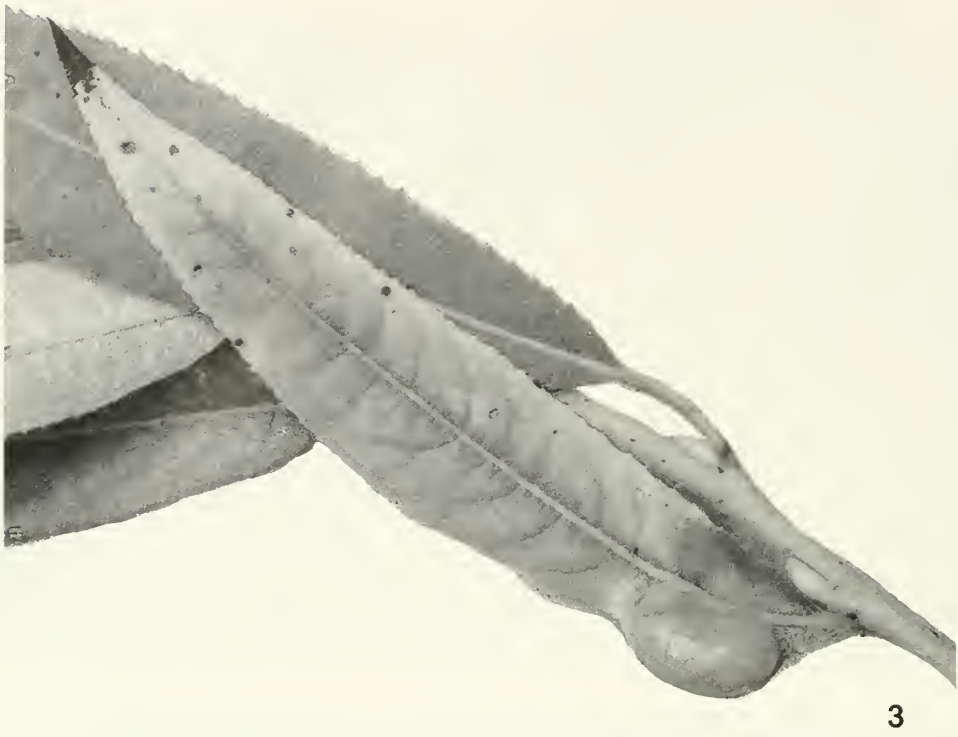


Fig. 3. Gall of *Pontania* (*Eupontania*) *gracilis* on *Salix sericea*, Milford, Otsego Co., N.Y.

the holotype revealed that this species belongs to the genus *Nematus* Panzer. The ovipositors of *Nematus* are normally broad and straight (Benson 1958, figs. 712–725), and those of *Pontania* and *Phyllocolpa* are usually slender and curved (Benson 1958, figs. 636–641). The slight ventroapicale margination of the sheath (Fig. 10) led to the placement of this species in *Phyllocolpa* by Smith and Fritz (1996). The correct combination is *Nematus acuminatus* (Marlatt), **n. comb.**

Pontania atra Marlatt 1896a: 37.

Type locality.—Michigan. The holotype is from "Ag. Coll. Mich.," and is presumably from East Lansing.

Type material.—Described from one female. The holotype female is labeled: "Ag. Coll. Mich. 4–21 90 62; Davis; Type female; Type No 1916 U.S.N.M.; Pontania atra n. sp. female." Deposited in the USNM.

Host plant.—Unknown.

Notes.—This species is currently placed as a synonym of *Amauronematus amentorum* (Förster) (Smith 1979). The latter, together with the related species inhabiting willow catkins, are now placed in a separate genus, *Pontoprista* Malaise.

Pteronus dubius Marlatt 1896a: 74.

Type locality.—Wellesley, Mass.

Type material.—Described from one male. The holotype is labeled: "Wellesley, Mass., March 29, 1890; Type male; Type No. 1937 U.S.N.M.; Pteronus dubius male." The genitalia are on a separate pin in a tube and with the label: "TYPE Pteronus dubius Marl." Deposited in the USNM.

Host plant.—Unknown.

Notes.—This species was correctly assigned to *Pontania* (Smith 1979). Males are difficult to place and generic placement is the best that can be done at present.

Pontania gracilis Marlatt, 1896a: 39.

Type locality.—Virginia.

Type material.—Described from two females and an undetermined number of galls. Lectotype female, here designated: "No 152x, Iss. Apr. 19. 86; Type female, Type No. 1919 U.S.N.M.; Pontania gracilis n. sp." Paralectotype: "No 152x, Iss. Apr. 19. 86; Type female, Type No. 1919 U.S.N.M." There are two dry galls with the following labels: "152x Va Sept. 29. 85"; one of them (Fig. 6) with the remnants of the leaf (the lower surface with sparse trichomes) and the label "gall on Salix sericea det G. Argus, 1996." The types and galls are in the USNM.

Host plant.— *Salix sericea* Marsh. (identified by G. Argus).

Notes.—This is a valid species of *Pontania* (*Eupontania*). The description of *P. gracilis* larvae and biology by Dyar (1897b) refers to *P. petiolaridis* Rohwer (see below). A typical gall of this species is shown in Fig. 3 (from Otsego Co., N.Y., collected by AGZ and R. Fritz).

Pontania nigrita Marlatt 1896a: 27.

Type locality.—Michigan. The holotype is labeled "Ag.Coll.Mich," presumably from East Lansing.

Type material.—Described from one female. The holotype was redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host plants.—According to Smith and Fritz (1996), the host plants are *Salix sericea, S. discolor* Muhl., and *S. eriocephala* Michx.

Notes.—This is a valid species of *Phyllocolpa* and belongs to the *leucosticta* group. Its larva and biology were described by Dyar (1897b) under the name *Pontania pallicornis* Norton.

Pontania pectoralis Marlatt 1896a: 31.

Type locality.—Algonquin, Illinois.

Type material.—Described from one female. The holotype was redescribed by Smith and Fritz (1996). Deposited in CUIC.

Host plant.—Unknown.

Notes.—This is a valid species, *Phyllocolpa pectoralis* (Marlatt).

Pontania populi Marlatt 1896b: 253.

Type locality.—New York, as given by Marlatt. The specimen described was reared by Dyar; Dyar (1897a) stated it was from Fort Lee, N.J.

Type material.—Described from one female. The holotype was redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host plant.— *Populus grandidentata* Michx.

Notes.—A valid species, *Pontania* (*Pontania*) *populi* Marlatt, belonging to the *crassispina* group. The larvae and biology were described by Dyar (1897a). It produces leaf rolls on the host creating a small swelling (procecidium) at the site of egg laying. There is more than one generation per year. The larvae eat the parenchyma and leave the upper cuticle intact, which is typical for species of the *crassispina* group. A very slight ventroapical indentation of the sheath (Fig. 11) and the leaf-folding habit led to the inclusion of this species in *Phyllocolpa* by Smith and Fritz (1996).

Pontania robusta Marlatt 1896a: 32.

Type locality.—"Michigan and District of Columbia (?)." The lectotype is labeled "Ag.Coll.Mich.," presumably East Lansing.

Type material.—Described from one female and one male. The lectotype, a female from Michigan, was selected and redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host.—*Populus tremuloides* Michx.

Notes.—This is a valid species of *Phyllocolpa* in the *leucapsis* group. The larva and biology were described by Dyar (1897b). It produces leaf folds on aspen, as was confirmed by Smith and Fritz (1996). There is one generation a year.

Pontania rugulosa Marlatt 1896a: 41.

Type locality.—Michigan.

Type material.—Described from two males, "one reared (?) from willow gall." The lectotype, here designated, is labeled: "O; 17; Collection C.V. Riley; Type male; Type No 1920 U.S.N.M.; Pontania rugulosa M. n.sp." There is a gall on the same pin, but it does not belong to the lectotype. Deposited in the USNM.

Host plant.—Willow (species unknown).

Notes.—This species belongs to *Pontania* (*Eupontania*) according to the shape of the mandibles, but we are not certain if it is a valid species because males are difficult to place. The gall lacks an exit hole, but the male has part of the pupal skin attached to the leg. It may have been reared from a similar gall, but not the gall on the pin. The gall on the pin is equally produced from both sides of the leaf, but it is practically without leaf remnants and the willow probably cannot be identified.

Pontania terminalis Marlatt 1896b: 253.

Type locality.—Near New York City. The specimens were from Dyar's collections and, according to Dyar (1897a), were from Van Cortland Park, New York City.

Type material.—Described from three females and two males. The female lectotype was selected and the species redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host plant.— *Salix sericea*, according to Smith and Fritz (1996). The host plant relationships of *P. terminalis* need to be confirmed. There is possibly more than one species under this name.

Notes.—The valid name is *Pontania* (*Pontania*) *terminalis* Marlatt, and it belongs to the *crassispina* group. The larvae and biology were described by Dyar (1897a). It produces leaf rolls on willow similar to *P. populi* except with a smaller swelling at the site of egg laying. The larvae eat parenchyma and leave the upper cuticle intact, which is typical for this species group. The slight ventroapical indentation of the sheath (Fig. 12) and leaf-folding habit led to the placement of this species in *Phyllocolpa* by Smith and Fritz (1996).

Species Described by Dyar

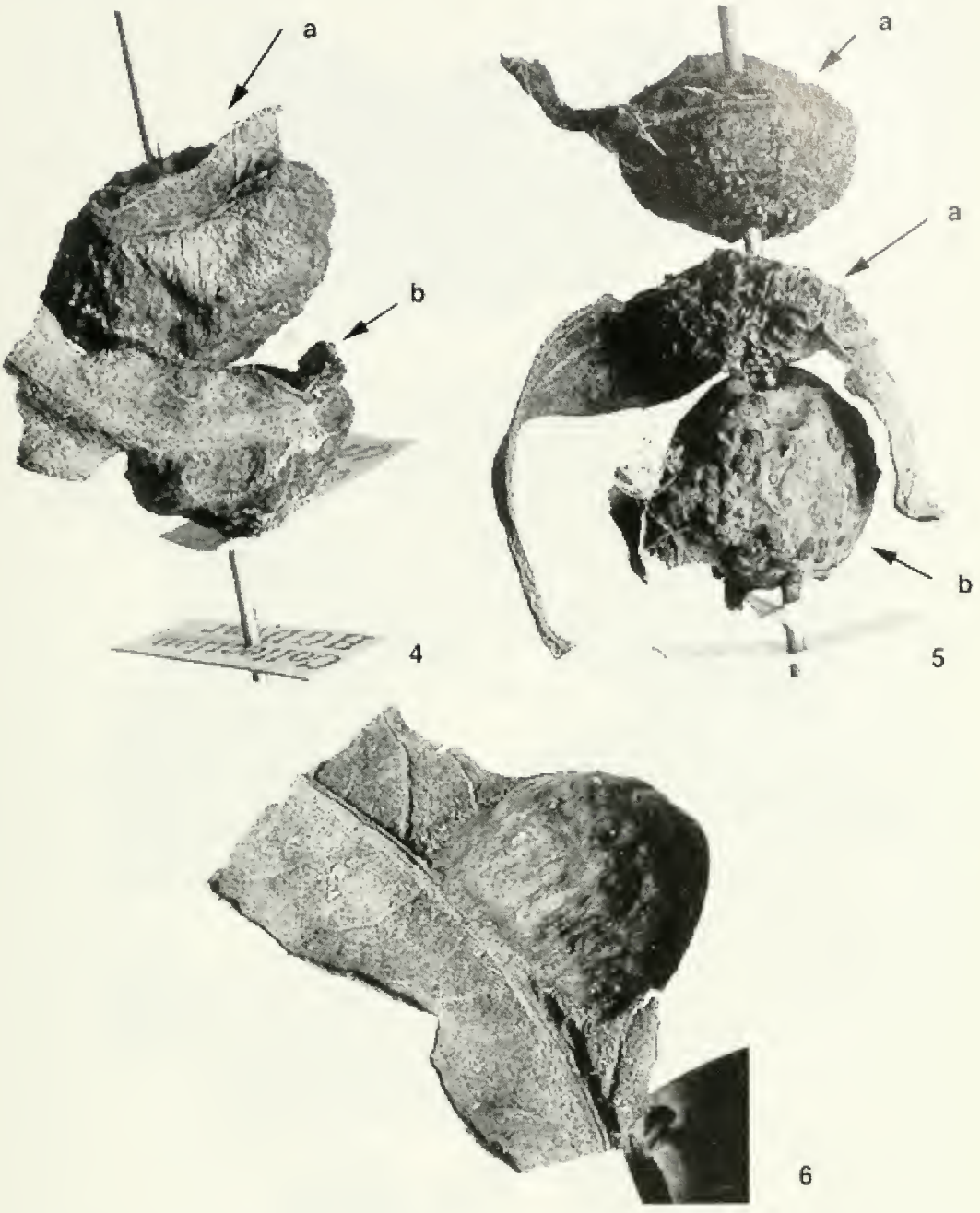
Dyar (1898) attributed the authorship of *Pontania consors, Pontania borealis,* and *Pteronus carpini* to Marlatt (1898), but Dyar's descriptions of these species precede those of Marlatt by about half a year. Marlatt (1898) cited "Dyar. N. Y. Ent. Soc., VI., June 1898, p. 121" in his descriptions. Therefore we change the authorship of the following names to Dyar: *Pontania borealis, Pontania consors,* and *Pteronus carpini.* We treat the adults reared from larvae described by Dyar as holotypes or lectotypes. *Pteronus carpini* is a valid species in the genus *Nematus* (Smith 1979).

Pontania borealis Dyar 1898: 121 (galls, larva).—Marlatt 1898: 302 (female).

Type locality.—Plattsburgh, N.Y., according to Dyar (1898).

Type material.—Dyar did not state the number of galls and larvae he reared. Marlatt described the reared adults from two females. The lectotype female, here designated, is labeled: "8S; Collection H. G. Dyar; Type No 4131 U.S.N.M.; Pontania borealis female Marl." Paralectotype:"8S; Collection H. G. Dyar; Pontania borealis Marl." There is also one similarly labeled specimen without Marlatt's identification label. Galls: There are two galls on a pin (Fig. 4) labeled: "8S; Collection H. G. Dyar; Type No 4131 U.S.N.M.; Pontania borealis gall Marl." An additional label is added: "upper gall: P. (Eu.) s-pomum, lower gall: P. (Eu.) s-desmodioides, A. Zinovjev det, 1997". There are three galls on another pin (Fig. 5) without Marlatt's identification label, but some of them probably also belong to the type series of *P. borealis.* The two upper galls are of *P.* (*E.*) *s-desmodiodes* (A. Zinovjev det. 1997, galls on *Salix humilis* det G. Argus, 1996; lower gall of *P.* (*E.*) *s-pomum*). Deposited in USNM.

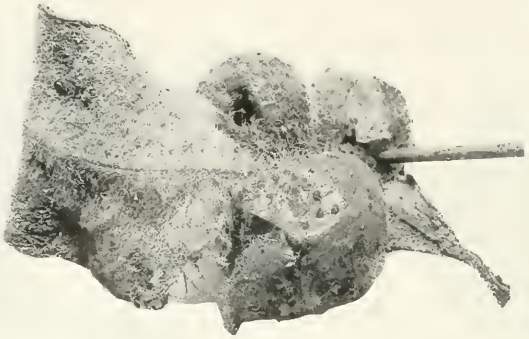
Host plant.— *Salix humilis* Marsh. as de-



Figs. 4–6. Galls of *Pontania* (*Eupontania*) spp. 4, *P.*(*E.*)? *s-ponum* (a) and *P.* (*E.*) *s-desmodioides* (type material of *P. borealis*) (b) on same pin. 5, *P.* (*E.*) *s-desmodioides* (a) and *P.* (*E.*) ? *s-ponum* (b) on same pin. 6, Type material of *P.* (*E.*) *gracilis* on *Salix sericea.*

termined by G. Argus (not *Salix sericea* as reported by Dyar).

Notes.—The valid name is *Pontania* (*Eupontania*) *s-desmodioides* (Walsh) (= *Pontania borealis* Dyar, **n. syn.**). Dyar's (1898) description of the galls is very similar to those described by Walsh (1866) for *P. s-desmodioides.* The host plant was misiden-



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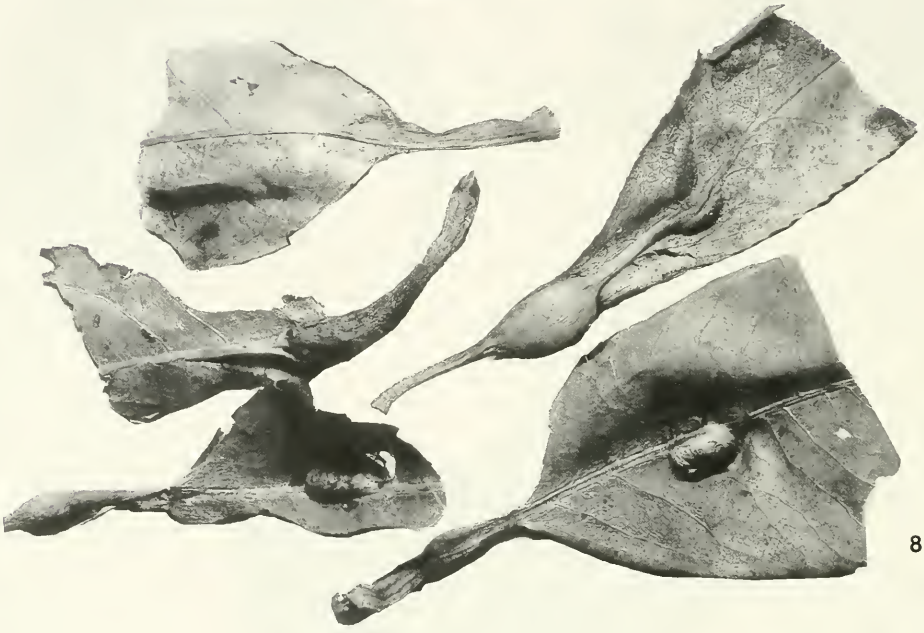

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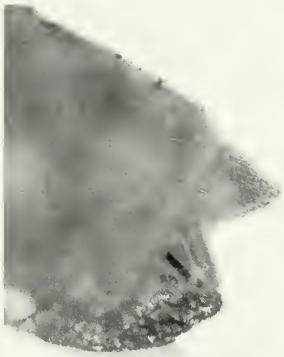
Figs. 7–9. Galls of *Pontania* (*Eupontania*) spp. 7, *P.* (*E.*) *consors*, from which type material was reared. 8, *P.* (*E.*) *lucidae*, from which the type material was reared. 9, *P.* (*E.*) *petiolaridis*, type material on *Salix petiolaris*.



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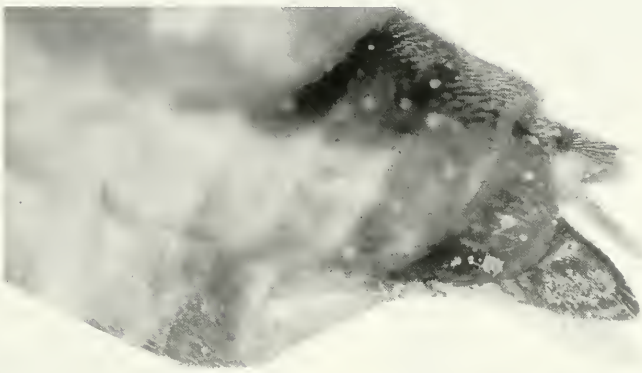

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Figs. 10–12. 10, Apex of abdomen and sheath of *Nematus acuminatus*. 11, Apex of abdomen and sheath of *Pontania populi*. 12, Lateral view of *P. terminalis*.

tified by Dyar. The remnants of leaves with the galls of this species collected by Dyar are shown in Figs. 4, 5. The leaf shape and pubescence of those associated with *P. s-desmodioides* is typical for *Salix humilis,* and the willow identification was confirmed by G. Argus. However, along with these galls of *P. s-desmodioides* (Figs. 4b, 5a), there are also two others on the same pins which appear to belong to *P. s-pomum* (Figs. 4a, 5b). A typical *P. s-pomum* gall is in Fig. 2. The remnants of the leaves attached to the latter two galls are glabrous and might be *Salix eriocephala* Michx., the host plant of *P. s-pomum.* However, none of the three reared females can be identified as *P. (E.) s-pomum.*

Pontania consors Dyar 1898: 121 (galls, larva).—Marlatt 1898: 302 (female, male).

Type locality.—Plattsburgh, N.Y.

Type material.—Dyar did not give the number of galls and larvae. Marlatt described adults from one female and two males. The lectotype female, here designated, is labeled: "8T; Collection H. G. Dyar; Type No 4132 U.S.N.M.; Pontania consors female Marl." Paralectotypes: 2 males, "8T; Collection H. G. Dyar; Type No 4132 U.S.N.M.; Pontania consors male Marl." Five galls from two leaves are on a pin labeled: "8T; Collection H. G. Dyar" (Fig. 7). There is also a cocoon in decayed wood with the label "8T; Pontania consors Marl." Deposited in the USNM.

Host plant.— *Salix humilis* as identified by G. Argus (not *Salix sericea* as reported by Dyar).

Notes.—This is a valid species, *Pontania (Eupontania) consors* Dyar. Dyar described the species as follows: "Galls found with the preceding on *S. sericea,* but gregarious, hairy and spherical. Near the base of the leaf, three or two together, rarely but one, exceeding the margin often by half the diameter of the gall; not evenly divided by the leaf, about one third or a little more above, two thirds below; pale greenish, often heavily marked and mottled with red above, paler below, rarely uniformly pale. Strongly silky hairy like the leaves below, less hairy or even smooth above; size 8.5–8.5–7 mm or as small as 5 mm in diameter." The host plant was misidentified by Dyar. The remnants of the leaf were identified by G. Argus, as in the preceding case (*P. borealis*), as *Salix humilis.* A. G. Zinovjev and H. Goulet collected galls of *P. consors* at Lake Jean Venne, Masham Co., Quebec, Canada (about 50 km N of Ottawa) in the fall of 1995 on *Salix humilis* (hostplant determined by G. Argus).

Species Described by Rohwer

S. A. Rohwer did not select single specimens as holotypes in his publications, even though he attached holotype or paratype labels and USNM type numbers to specimens of each species he described. Therefore, we designate lectotypes where necesary.

Pontania amentivora Rohwer 1915: 209.

Type locality.—Falls Church, Virginia.

Type material.—Described from four females. The lectotype female (with a cocoon on the same pin), here designated, is labeled: "10128 Hopk. U.S.; reared May 13 13; Falls Church, Va; S.A. Rohwer Coll.; Type female No. 18313 U.S.N.M.; Pontania amentivora Type Roh." Deposited in USNM.

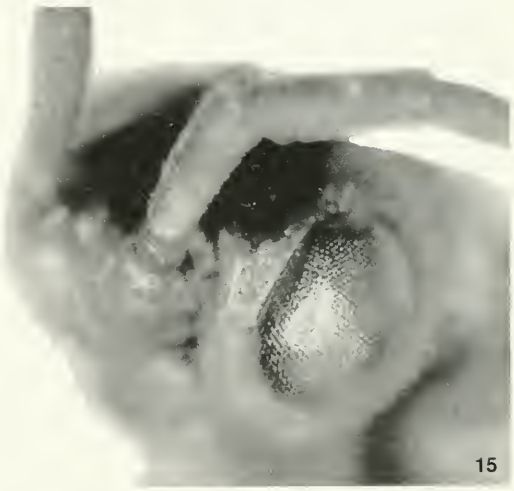
Host plant.— *Salix* sp.

Notes.—According to Rohwer "this species lives, in the larval stage, in the pistillate catkins of a small species of *Salix* and causes the destruction of the ovaries and the premature forming of 'cotton'." This species is currently placed as a synonym of *Amauronematus amentorum* (Förster) (Smith 1979). The catkin feeders, including this and some related species previously placed in *Amauronematus* Konow belong in the genus *Pontoprista* Malaise.

Pontania crassicornis Rohwer, 1912: 241.

Type locality.—Toronto, Ontario, Canada.

Type material.—Described from one



Figs. 13–15. 13, Lateral view of *P. pumila*. 14, Dorsal view of head of *Phyllocolpa crassicornis*, holotype. 15, Anterolateral view of head of *P. crassicornis*, holotype.

male. The holotype is labeled "ex galls on Salix humilis; Toronto Ont; A. Cosens. Coll.; Type male no. 14572 U.S.N.M; Pontania crassicornis TYPE male Roh.; Pontania (Phyllocolpa) crassicornis Rohwer, det. A.Zinovjev 1996." There are also many dry leaves with galls labeled: "Pontania crassicornis Roh.? Toronto, Ontario, Canada. Cosens; galls of Pontania (Eupontania) consors Dyar, A. Zinovjev det, 1997." Deposited in the USNM.

Host plant.— *Salix humilis* (original identification confirmed by G. Argus).

Notes.—The valid combination is *Phyllocolpa crassicornis* (Rohwer), **n. comb.** The leaves with the galls are *Salix humilis*

and the galls those of *P. consors*. However, the holotype is a typical leaf roller of the *Phyllocolpa leucapsis* group. The mandibles are asymmetric, the left one in lateral view with a swollen base and a thin blade-like apex, distinctly carinate on the outer surface, and the antennal hollows are glabrous, shining, and keeled laterally (Figs. 14, 15). Rohwer (1912) mentioned its close relationship to *Pontania robusta* Marlatt, which is known to produce leaf folds on aspen. Although we are not able to distinguish the males of *Pontania* and *Phyllocolpa,* we consider this species to be a valid one.

Pontania leavitti Rohwer 1910: 199.

Type locality.—Nerepis, New Brunswick.

Type material.—Described from one female. The holotype was redescribed by Smith and Fritz (1996). Deposited in the USNM.

Host plant.— *Salix sericea,* according to Smith and Fritz (1996).

Notes.—A valid species of *Phyllocolpa* in the *leucosticta* group. The larvae form leaf rolls on *Salix sericea* and perhaps some other willows.

Pontania lucidae Rohwer, 1912: 242.

Type locality.—Toronto, Ontario, Canada.

Type material.—Described from "Males and females bred from galls on *Salix lucida,* by A. Cosens." The number of specimens is not stated. The lectotype female, here designated, is labeled: "ex galls on Salix lucida: Toronto Ont; A. Cosens Coll.; Type female No. 14571 U.S.N.M.; Pontania lucidae TYPE female Roh." Paralectotypes: 4 females, 5 males with labels as on the lectotype, except "Paratype No. 14571 U.S.N.M." One male bears the label "Pontania lucidae male allotype Roh." One of the males does not have a red type label, but perhaps it also belongs to the type series. There are remnants of six dry leaves with galls (Fig. 8) labeled "Pontania lucidae Roh. Salix lucidae. Cosens. Toronto, Canada." Deposited in the USNM.

Host plant.— *Salix lucida* (original identification confirmed by G. Argus).

Notes.—A valid species in *Pontania* (*Eupontania*), closely related to *Pontania consors* as was stated by Rohwer. The examined leaves of *Salix lucidae* bear only a few typical leaf galls associated with midribs. The rest of the galls in this sample might rather be called petiole or midrib galls (Fig. 8). We are not sure if all of these galls belong to the species described by Rohwer or if some of them are *Euura* galls.

Pontania petiolaridis Rohwer 1917: 19.

Type locality.—Toronto, Ontario, Canada.

Type material.—"Described from a number of females and males reared by A. Cosens from galls on Salix petiolaris." Numbers of specimens were not given. The lectotype female, here designated, is labeled: "Salix petiolaris; Toronto Ont; A. Cosens Coll.; Type female No. 20697 U.S.N.M.; Pontania petiolaridis TYPE female Roh." Paralectotypes: 4 females, 2 males with the same labels, except "Paratype No. 20697 U.S.N.M." One male bears the label "Pontania petiolaridis male allotype Roh." There are many dry galls with remnants of leaves and a label: "Paratype No. 20697 U.S.N.M.; Pontania petiolaridis TYPE galls Roh." Deposited in the USNM.

Host plant.— *Salix petiolaris* Sm. (identification confirmed by G. Argus).

Notes.—This is a valid species in *Pontania* (*Eupontania*), is very closely related to *P. gracilis,* and has galls (Fig. 9) similar to those of *P. gracilis* (Figs. 3, 6). The galls and biology were described by Cosens (1917) and probably by Dyar (1897b) under the name *Pontania gracilis* (host-plant "*Salix petiolata*") from Van Cortland Park, New York City, and Gouverneur, N.Y., on "Salix petiolata." The name "*petiolata*" is obviously a misprint for *S. petiolaris* (G. Argus, personal communication). Also, the remnants of leaves with the galls are gla-

brous and might belong to *S. petiolaris*. A. G. Zinovjev reared this species from galls collected by R. Vanderkam near Ottawa, Ontario, in 1995.

Pontania pumila Rohwer 1910: 198.

Type locality.—St. John, New Brunswick.

Type material.—Described from one female and one male. The lectotype female, here designated, is labeled: "St. John, New Brunswick" (female, July 14). Paralectotype: male, "Nerepis NB 22 Jul; AG Leavitt; TYPE male No 12920 U.S.N.M.; Pontania pumila Roh. TYPE male." Deposited in the USNM.

Host plant.—Unknown.

Notes.—This is a valid species, *Pontania* (*Pontania*) *pumila* Rohwer. It very likely belongs in the leaf-rolling *crassispina* group. The shape of the sheath (Fig. 13) and ovipositor are typical for this group.

Acknowledgments

We thank G. Argus, Ottawa, Ontario, Canada, for identification of the willows. E. R. Hoebeke kindly loaned the type of *Pontania pectoralis* Marlatt. Robert Fritz, Vassar College, Poughkeepsie, N.Y., helped with collection of galls in Otsego Co., N.Y. Part of this work was supported by a Smithsonian Institution Short-Term Visitors Grant to A. G. Zinovjev. We thank the following for review of the manuscript: N. Schiff, USDA, Forest Service, Stoneville, Miss., and M. A. Solis and M. E. Schauff, Systematic Entomology Laboratory, USDA, Washington, DC.

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DESCRIPTION OF IMMATURE STAGES OF *PLATYVELIA BRACHIALIS* (STÅL) (HETEROPTERA: VELIIDAE)

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Abstract.—The five immature instars of the broad-shouldered waterstrider, *Platyvelia brachialis*, are described for the first time. Of three characters considered diagnostic for adult *Platyvelia* only one, patches of silvery setae on the abdominal dorsum, was observed on immatures of *P. brachialis*.

Key Words: Broad-shouldered waterstriders, *Platyvelia brachialis*, Veliidae, Heteroptera, immature insects

During a collecting trip to northeastern North Carolina in August 1994, the two senior authors collected a complete series of immature instars for the veliid species *Platyvelia brachialis* (Stål). We here provide the first description of the five immature instars of this species. Readers wishing to learn more about the adults of *Platyvelia brachialis* should consult Polhemus and Polhemus (1993) and the references therein. Excellent, more general treatments of veliids can be found in Andersen (1982), Smith (1988), and Schuh and Slater (1995).

MATERIALS AND METHODS

Specimens were collected along the banks of stagnant bodies of water at the following localities in northeastern North Carolina: Washington Co., Thirty Foot Canal, near junction of Thirty Foot Canal Rd. and Tom Pepper Rd., 12, 13 August 1994; Washington Co., ca. 1 km. E. of Creshell near junction of Old Cherry Rd. and Springhill Rd., 12 August 1994; Tyrell Co., Batavia Canal, ca. 2 km N. or Lake Phelps, 13 August 1994. They were collected by disturbing the vegetation along the banks. The veliids would then walk out onto the water, away from the banks, at which time they were easily collected from the water surface with an aspirator. In addition to the immatures described below, 27 adult males and 24 adult females were collected. All the adults were macropterous.

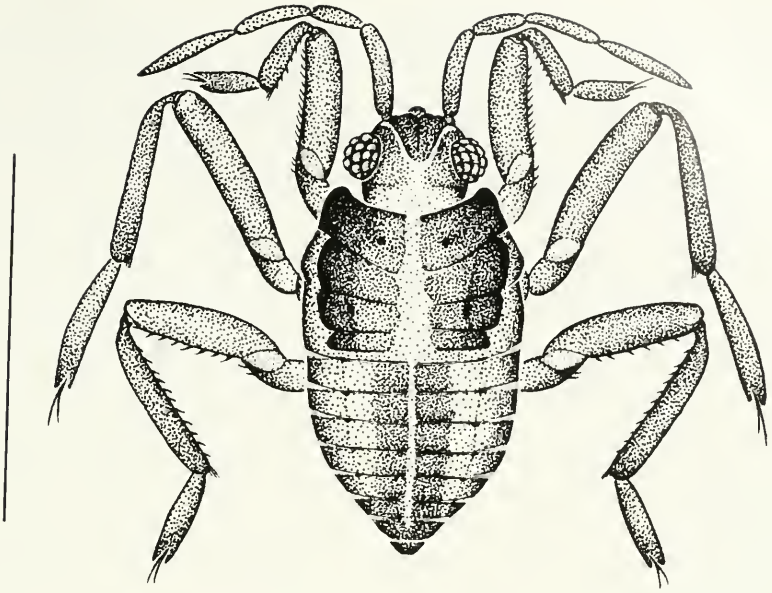
Descriptions were based on 3 first, 4 second, 5 third, 6 fourth, and 4 fifth instar specimens. Dorsal habitus illustrations were produced using a camera lucida mounted on a Zeiss Stemi SV6 stereomicroscope.

Voucher specimens have been deposited in the first author's private collection.

DESCRIPTIONS

First instar (Fig. 1).—Length, 1.25 mm ± 0.09 mm; width, 0.61 mm ± 0.03 mm. Body elongate and elliptical, greatest width at mesothorax; general ground color ochreous; covered with dense, short setae.

Head declivent, dorsally brown, ventrally ochreous, vertex with dark median stripe; anteclypeus protruding, rounded anteriorly; remainder of head excluding eyes subrectangular; ecdysial lines ochreous, Y-shaped, stem wider than arms, arising from poste-



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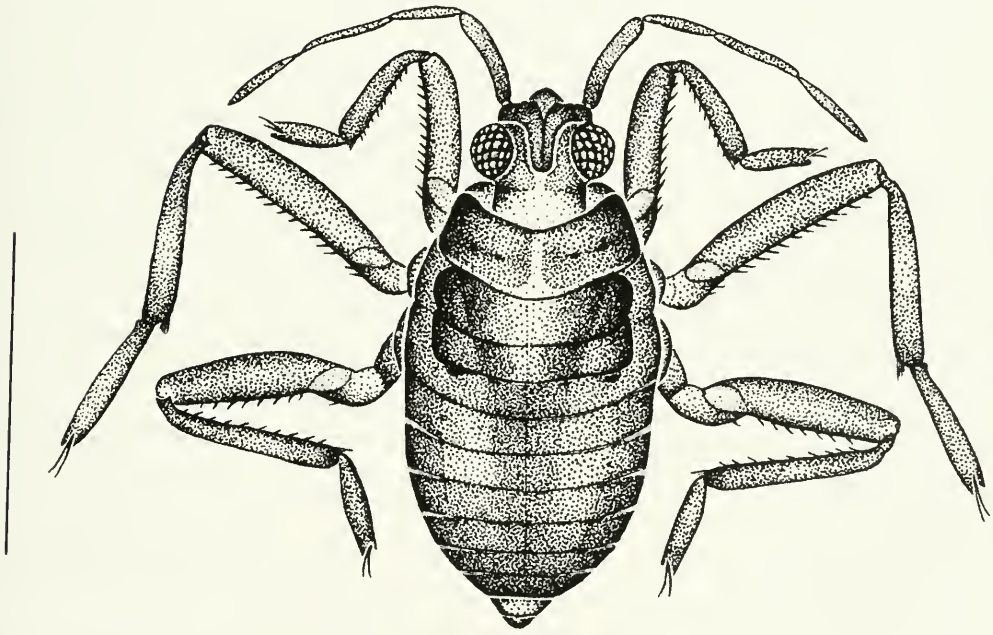

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Figs. 1–2. *Platyvelia brachialis*. 1, First instar. 2, Second instar. Scale bar = 1 mm.

rior margin of head, arms extending to anteroinferior margin of eyes. Eyes globose, red, separated by ca. 1.6× width of eyes; ocular setae absent. 3 pairs of trichobothria present, 1st pair just posterior to anteclypeus, 2nd pair posterolateral to 1st pair, 3rd pair just medial to inner margin of eyes. Antenna 4-segmented, brown with segments 1 and 2 darker than 3 and 4; segment 1 curved, segment 2 shortest, segment 4 longest and tapered apically. Beak 4-segmented, segments 1–3 ochreous, 4 brown; segment 2 shortest, segment 3 longest, segments 1 and 4 subequal.

Thoracic nota each with pair of sclerotized, brown subrectangular plates covering most of dorsum, each wider laterally, separated medially by an ochreous ecdysial membrane which widens posteriorly; pronotal plates extending further laterally than meso- and metanota, mesonota extend only slightly further laterally than metanota. Dark fovea present on each pronotal plate roughly in line with anteromedial corner of eye; shallow oblique depression lateral to fovea extending anterolaterally. Meso- and metanota with dark longitudinal markings in line with posteromedial corner of eyes. Thoracic pleura and sterna ochreous, membranous; supracoxal lobes sclerotized and pigmented brown.

Legs brownish dorsally, ochreous ventrally, setose throughout; mesothoracic leg longest. Prothoracic leg somewhat raptorial; coxa globose distally, subequal in length to trochanter; trochanter ventral margin longer than dorsal, subequal in length to tarsus, 5–7 spines on ventral surface distally; femur slightly curved, ochreous at distal tip, ca. 1 ⅓× longer than tibia, proximal ¾ of ventral margin with double row of spines; tibia slightly curved, row of short, thick spines anteroventrally, longer, thinner spines posteroventrally, tuft of hairs anterodistally, grooming comb distally and posteroventral; tarsi straight, 1-segmented, subequal in length to trochanter, short, paired claws subapical. Mesothoracic coxa globose distally, subequal in length to trochanter; trochanter without ventral spines, ca. ½ length of tarsus; femur slightly curved, ochreous at distal tip, double row of spines absent, subequal to slightly longer than tibia; tibia straight, ventral spines absent, anterodistal hair tuft present but less dense than on protibia, grooming comb present; tarsus straight, ca. ¾ length of tibia, subapical claw slender, longer than protarsal claw. Metathoracic coxa elongate, subrectangular, constricted proximally but not rounded distally, shorter than trochanter; trochanter without ventral spines, subequal in length to tarsus; femur slightly curved, ochreous at distal tip, subequal to slightly longer than tibia, single row of 4–6 short, thick spines ventral; tibia straight, single row of 13–15 thin recurved spines on ventral surface, anterodistal hair tuft absent, grooming comb present, tarsus straight, ca. ½ length of tibia, subapical claw similar to mesotarsal claw.

Abdomen ochreous. Tergum 1 with pair of rectangular mediotergites widely separated by medial ecdysial membrane, laterotergites absent. Terga 2–8 with pair of rectangular mediotergites, lateral margins slightly lateral to medial margins of 1st mediotergites, narrowly separated by medial ecdysial membrane; two pairs of laterotergites present, the first small, narrowly and irregularly elliptical, found on anterior margin of segments, the second minute, located intrasegmentally, distal to first, both absent on segment 8; distance between medio- and laterotergites decreases posteriorly. Spiracles present dorsally on segment 1, laterally on segments 2–7. Minute pleurites present on segments 2–7. Venter mostly membranous, pair of sclerites present medially on segment 8. Segment 9 cone-shaped, sclerotized dorsally and laterally. Segment 10 only visible ventrally, enclosed dorsally and laterally by segment 9.

Second instar (Fig. 2).—Length, 1.70 mm ± 0.05 mm; width, 0.74 mm ± 0.04 mm.

Ground color slightly darker than first. Antennal tubercles more distinct.

Pair of dark foveae present on each pro-

notal plate, medial fovea in line with anteromedial margin of eye, lateral fovea present in medial end of oblique depression, in line with lateral margin of base of antennae, area between foveae of each plate slightly depressed. Meso- and metanotal plates with dark, narrowly U-shaped longitudinal markings in middle, open anteriorly.

Ventral surface of legs brownish. Prothoracic femur ca. 1.4× length of tibia; faint yellow band in distal ⅓. Tibia with faint ochreous band in middle third. Mesothoracic trochanter with pair of denticles on distoventral aspect. Femur with faint yellow band in distal third. Tibia with faint ochreous band in middle third; double row of spines present, shorter and fewer than that of profemur. Tarsus ca. 0.8× length of tibia. Metathoracic trochanter with 3–4 short spines on distoventral aspect. Femur with double row of 7–9 ventral spines, dorsal row longer, more robust; faint yellow band in distal half. Tibia with faint ochreous band in middle ¼.

Abdominal mediotergites of segment 1 lightly pigmented, subrectangular, narrowly separated by ecdysal line; mediotergites of segments 2–8 greatly reduced, taking on an irregular elliptical shape, located anteriorly along intersegmental fold; all mediotergites forming a parallel row in line with the medial prothoracic foveae. Laterotergites present on segment 1 as small elliptical disks along intersegmental membrane with metathorax. Segment 9 with ecdysial line.

Otherwise similar to first instar.

Third instar (Fig. 3).—Length, 2.10 mm ± 0.16 mm; width, 0.95 mm ± 0.04 mm.

Ground color darker. Eyes separated by ca. 1.2× width of eye. Antennal segment 1 subequal to segment 4.

Posterior margin of pronotum extends posterior at midline. Lateral foveae in line with posteromedial margin of eyes. Mesonotal wing pads present, extending posteriorly ca. ½ length of metanotum. Metanotal wing pads extend ca. ½ length of first abdominal segment.

Leg bands more distinct; proximal ½ of tarsi ochreous. Prothoracic trochanter with 8–12 spines on distoventral surface; femur ca. 1.6× longer than tibia, spines extend nearly length of ventral surface. Mesothoracic tarsus ca. 0.7× length of tibia. Metathoracic femur with double row of 9–11 short, thin spines; femur slightly longer than tibia.

Sternite on abdominal segment 8 heavily setose.

Otherwise similar to second instar.

Fourth instar (Fig. 4).—Length, 3.04 mm ± 0.18 mm; width 1.13 mm ± 0.10 mm.

Body more elongate, greatest width at metathorax. Ground color darker. Eyes separated by ca. 1.6× width of eyes. First antennal segment ca. 1.4× length of fourth segment; darker in proximal ⅓. Second antennal segment with faint yellow band in proximal ½.

Mesothoracic wing pad nearly extends to posterior border of metanotum; metathoracic wing pad nearly extends to posterior border of first abdominal segment.

Mesothoracic tarsus ca. 0.6× length of tibia. Metathoracic tarsus ca. 0.4× length of tibia.

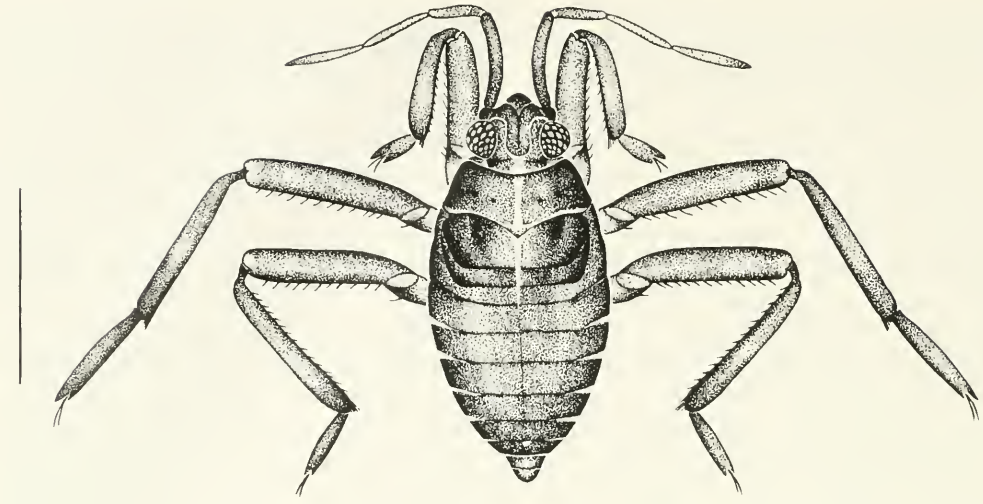
Thin patch of silvery pubescence present on distolateral margins of abdominal segments 2–7; ecdysal line forming ovate patch at anterior margin of segment 7, a smaller pair of ochreous spots lateral to ecdysal patch between the medio- and lateral tergites. Medial ½ of dorsal surface segment 8 ochreous; sexual differentiation apparent on ventral sternite of segment 8

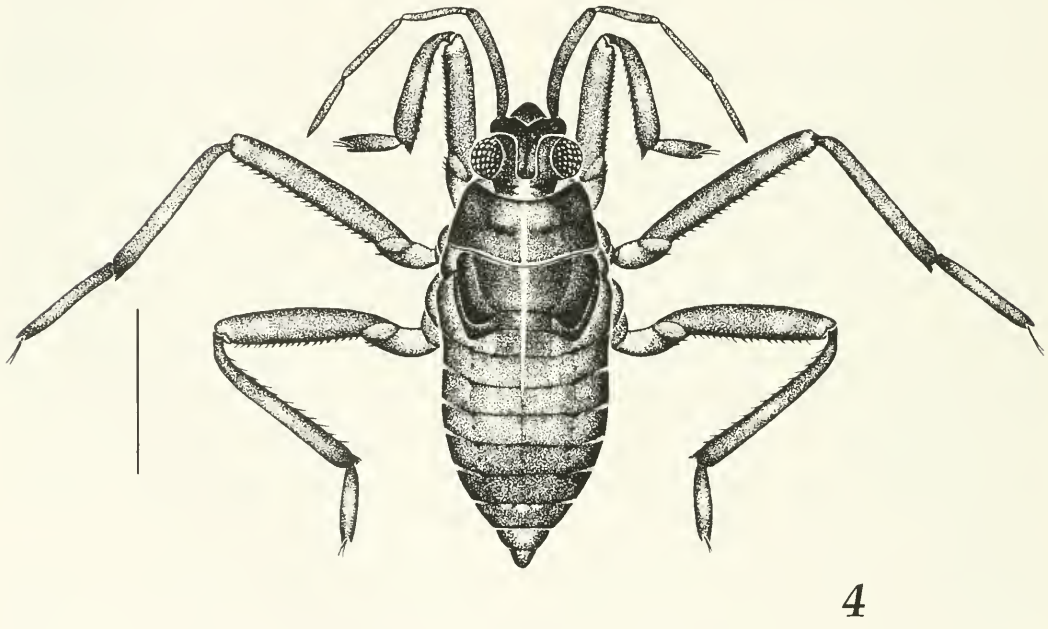
Otherwise similar to third instar.

Fifth instar (Fig. 5).—Length, 4.16 mm ± 0.23 mm; width, 1.48 mm, ± 0.10 mm.

Ground color darker, patterns more distinct. Antennal tubercles more distinct, nearly black; anteclypeus, postclypeus, and posterior margin of head nearly black. Eyes separated by 1.4× width of eyes. First antennal segment ca. 1.6× length of segment 4; segments 2 and 3 subequal.

Pronotum with dark brown markings extending anterolaterally from lateral foveae to anterior margin of pronotum and poste-





Figs. 3–4. *Platyvelia brachialis*. 3, Third instar. 4, Fourth instar. Scale bar = 1 mm.

riorly ⅔ the length of the lateral margin. Posterior ⅓ raised, quadrate and widened laterally. Midline elevated, reaching highest point at posterior margin.

Wing pad darker, more developed. Mesonotal pad with a broad, setose, semilunar elevation in medial ¾; pads extend posteriorly ca. ¾ length of abdominal segment 1, nearly covering metanotal pad. Distal tip of metanotal pad curved laterally, extending just distal to mesonotal pad.

Prothoracic femur ca. 1.2× length of tibia. Tibia ca. 2.5× length of tarsi, yellow band on posterior of proximal ¼; anterior

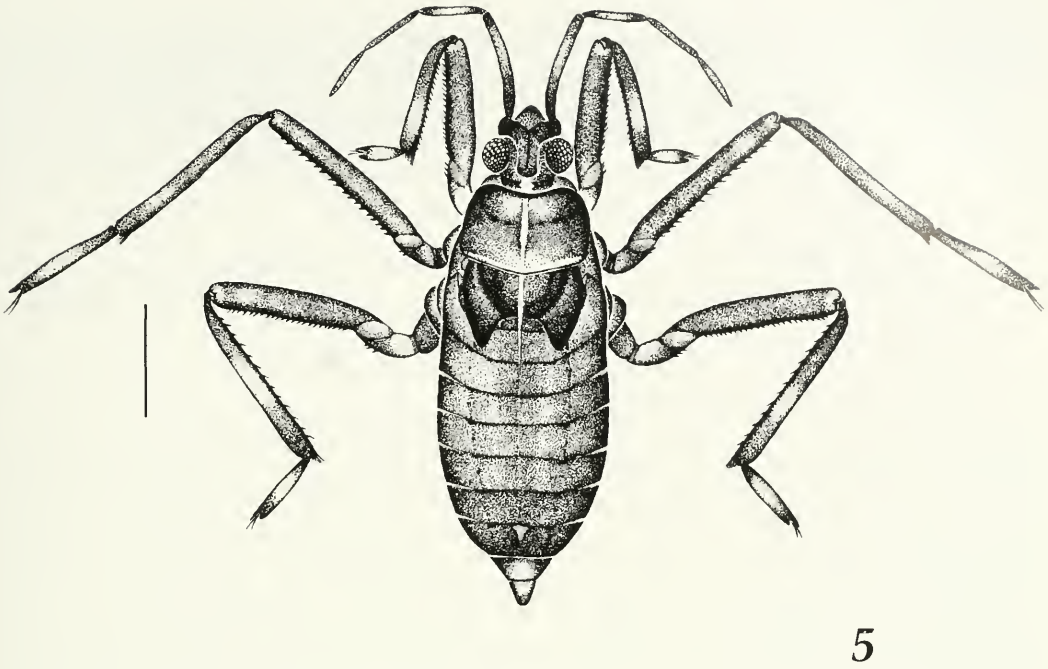


Fig. 5. *Platyvelia brachialis.* fifth instar. Scale bar = 1 mm.

surface yellow. Mesothoracic tibia with yellow band on posterior of proximal ¼; anterior surface yellow. Metathoracic tibia ca. 4.3× length of metatarsus; yellow band in proximal ¼.

Pubescence present along distolateral margins of abdominal segments 2–7 more distinct; additional pubescence present in random patterns along dorsal surface of segments 3–7. Segment 7 with dark yellow ovate spot present along anterior portion of ecdysal line. Segment 8 with anterior margin dark yellow, expanding along ecdysal line posteriorly; ventral aspect completely covered by sternites. Segment 9 usually with most of dorsal surface yellow.

Otherwise similar to fourth instar.

Discussion

Polhemus and Polhemus (1993) list three apomorphies for the genus *Platyvelia.* The first, opposing metasternal and mesoacetabular tubercles, are not present on immature specimens of *P. brachialis.* This is therefore an adult character. The second apomorphy, silvery setae on the abdominal dorsal surface (and on the hemelytra of winged adults), begins in the 4th instar, but only as small intersegmental areas between segments 2–7. Larger areas of silvery setae appear on the dorsal abdominal surface of instar 5, but these are not present in a distinct pattern. The final apomorphy is the lack of ocular setae, a trait shared with *Steinovelia.* We found no evidence of ocular setae in any instar. Thus, of three characters considered diagnostic for adult *Platyvelia* only one, patches of silvery setae on the abdominal dorsum, was observed on immatures of *P. brachialis.*

Acknowledgments

We thank John T. Polhemus and an anonymous reviewer for their critical review of the manuscript.

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CRASPEDOLEPTA EAS (MCATEE) AND *TRIALEURODES PHLOGIS* RUSSELL (HEMIPTERA: STERNORRHYNCHA: PSYLLIDAE AND ALEYRODIDAE): NEW DISTRIBUTIONAL AND HOST-PLANT RECORDS OF TWO LITTLE-KNOWN *PHLOX* SPECIALISTS

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Abstract.—The psyllid *Craspedolepta eas* (McAtee) and the whitefly *Trialeurodes phlogis* Russell are seldom-collected, univoltine specialists on *Phlox* species (Polemoniaceae), especially moss phlox, *P. subulata* L., in shale barrens. *Craspedolepta eas* is reported for the first time from Maryland, North Carolina, and South Carolina, with additional records given for Virginia and West Virginia. *Phlox nivalis* Lodd. is a new host of *C. eas*. The whitefly *T. phlogis*, previously known only from the type locality in Virginia, is newly recorded from Maryland, Pennsylvania, South Carolina, and West Virginia, with additional records given for Virginia. *Phlox nivalis* also is a new host of this aleyrodid.

Key Words: Insecta, monophagy, distribution, shale barrens

Moss phlox (*Phlox subulata* L.; Polemoniaceae) is a mat-forming, somewhat woody (suffruticose) perennial that harbors a diverse insect fauna, especially in mid-Appalachian shale barrens and outcrops. Its fauna includes two recently described species (Henry 1979, Russell 1993) and several undescribed species, as well as specialist herbivores whose association with phlox became known only with recent attention to this plant (Wheeler 1994; 1995a,b). Herein, I provide new distributional and host-plant data for two little-known sternorrhynchans that are phlox specialists.

Craspedolepta eas (McAtee)

This psyllid was described from Maryland in the vicinity of Plummers Island and from Great Falls (McAtee 1918). No additional records were available, nor were host relationships known, until Wheeler (1994) reported it from *Phlox* species in Illinois, Missouri, Pennsylvania, Virginia, and West Virginia. *Craspedolepta eas* develops on the narrow-leaved *P. subulata* in shale barrens and on broader-leaved phloxes, *P. divaricata* L. and *P. stolonifera* Sims, of more erect growth habit in moist woods. Nymphs of this univoltine psyllid overwinter at the base of their hosts and in spring resume feeding on stems near ground level. Adults begin to appear in early to mid-April and are present until mid- to late May. Infested hosts are most readily detected by looking for the psyllid's white, waxy secretions and honeydew in the crowns of moss phlox, or on basal stems in the case of more erect, herbaceous species of *Phlox* (Wheeler 1994).

The numbers in parentheses below refer to adults.

Records.—MARYLAND: Allegany Co., High Germany shale barren E. of Little Or-

leans, 6 May 1994 (1); Oldtown shale barren, 6 May 1994 (2). Washington Co., Boy Scout shale barren, Sideling Hill Wildlife Management Area, 6 & 15 May 1994 (>10). NORTH CAROLINA: Granville Co., Rt. 15, 0.6 km S. of Bullock, 29 Apr. 1997 (4). SOUTH CAROLINA: York Co., Blackjacks Heritage Preserve, S. of Rock Hill, 20 Apr. 1997 (3). VIRGINIA: Mecklenburg Co., Rt. 15 at State Line Rd., 1.3 km N. of North Carolina state line, 29 Apr. 1997 (5); Rockingham Co., Forest Service Rd. 87, George Washington National Forest, W. of Fulks Run, 18 May 1994 (1); Shenandoah Co., Edinburg Gap, 4 km E. of Edinburg, 30 Apr. 1994 (3). WEST VIRGINIA: Pendleton Co., SE. of Upper Tract, 24 Apr. 1994 (1).

Remarks.—Most of the new records of *C. eas* are from the Valley and Ridge Physiographic Province except those from North Carolina, South Carolina, and Mecklenburg County, Virginia, which extend the known distribution to the Piedmont. The host plant in the Piedmont was the narrow-leaved *P. nivalis* Lodd., a new host record for this psyllid. For all other new distributional records, the host was *P. subulata.*

Trialeurodes phlogis Russell

This whitefly was described from the Short Mountain shale barren near Mount Jackson, Va., on the basis of pupae I collected on *P. subulata* in mid-April 1991 and 1992 (Russell 1993). *Trialeurodes phlogis* has remained known only from the type locality.

Taxonomy of the Aleyrodidae is based on pupae; adults, therefore, cannot be identified with certainty. In the case of *T. phlogis,* the adults I collected from mat-forming phloxes are almost certainly those of this species. My initial observation of adults on *P. subulata* at Shanks, W. Va., in late April led Louise Russell to suspect that the whitefly involved might be an uncommon species; an early-season emergence of adults is atypical in the genus *Trialeurodes* (L.M. Russell, personal communication). *Trialeurodes phlogis* is the only aleyrodid known from wild phloxes, Britton's (1902) record of the greenhouse whitefly, *T. vaporariorum* (Westwood), from *Phlox* likely pertaining to plants in a greenhouse or garden (Russell 1993). Moreover, adults collected from phloxes of prostrate growth habits are gray, with dark markings on the forewings, matching the appearance of those I reared from pupae on foliage of *P. subulata* at the type locality of *T. phlogis.*

The numbers in parentheses below refer to adults unless otherwise noted.

Records.—MARYLAND: Allegany Co., High Germany shale barren, E. of Little Orleans, 6 May 1994 (1). PENNSYLVANIA: Chester Co., Unionville serpentine barrens, NE. of Unionville, 14 May 1994 (1). SOUTH CAROLINA: Pickens Co., nr. Todds Creek S. of Six Mile, 11 Apr. 1998 (2); York Co., Rt. 77 N. of junc. Rt. 901, S. of Rock Hill, 18 Apr. 1992 (1). VIRGINIA: Alleghany Co., Rt. 18, 17 km S. of Covington, 6 May 1990 (1); Bath Co., Rt. 678, Fort Lewis shale barren nr. Cowpasture River, 30 Apr. (2) & 20 May 1994 (3); Mecklenburg Co., Rt. 15 at State Line Rd., 1.3 km N. of North Carolina state line, 29 Apr. 1997 (1). WEST VIRGINIA: Greenbrier Co., Kates Mountain, S. of White Sulphur Springs, 6 May 1990 (2), 12 May 1991 (1 pupal case), 1 May 1994 (2); Whites Draft Rd., E. of Alvon, 1 May 1994 (3); Hampshire Co., Rt. 220, S. of Purgitsville, 14 May 1989 (2); Rt. 50, Shanks, 29 Apr. (>20) & 14 May 1989 (>10).

Remarks.—The host plant from which adults were collected was *P. subulata* except in Mecklenburg County, Virginia, and in South Carolina, where *P. nivalis* was the host. This plant is a new host record for *T. phlogis.*

Trialeurodes phlogis is a characteristic, though obscure, insect of mid-Appalachian shale barrens and shale outcrops. I also found it on *P. subulata* in a Pennsylvania serpentine barren. *Phlox nivalis* was a host in the Piedmont of Virginia and South Carolina. The pupae are difficult to find on the

upper or lower surfaces of the needlelike leaves of *P. nivalis* or *P. subulata.* Adults can be collected by shaking mats of host phloxes over a pan or tray. Unlike the psyllid *C. eas,* which occurs on phloxes of prostrate and erect growth habits, *T., phlogis* has been found only on mat-forming phloxes.

On the basis of my observations at the type locality in Virginia, *T. phlogis* is a univoltine whitefly. It overwinters as a third-stage larva (and possibly also as a pupa), with the adults emerging during the latter half of April. Adults are present until mid- to late May.

Acknowledgments

I am grateful to Louise Russell (USDA, Systematic Entomology Laboratory) for describing the new whitefly species found on phlox and to Gary Miller (USDA, Systematic Entomology Laboratory) for depositing voucher material of both species in the National Museum of Natural History, Beltsville, Md. For providing directions to sites with *Phlox nivalis* or *P. subulata,* facilitating the process of obtaining collecting permits, or accompanying me in the field, I thank Steve Bennett (South Carolina Department of Natural Resources), Ashton Berdine (The Nature Conservancy of Maryland), Richard Hoffman (Virginia Museum of Natural History), Carl Keener (Pennsylvania State University), John Nelson (University of South Carolina), Tom Rawinski (Massachusetts Audubon Society), and Doug Samson (The Nature Conservancy of Maryland). My colleague Peter Adler (Clemson University) provided useful suggestions for improving the manuscript.

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A NEW SPECIES OF *CRASPEDOXANTHA* BEZZI FROM TANZANIA AND A REVISED PHYLOGENY FOR THE GENUS (DIPTERA: TEPHRITIDAE)

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Abstract.—***Craspedoxantha yarivi*, n. sp.,** is described from specimens collected on, and reared from, *Vernonia calvoana* ssp. *usambarensis* C. Jeffrey (Asteraceae), in the western Usambara Mountains, Tanzania. The species is included in a refined phylogeny for the genus in which the previously proposed arrangement of two species groups remains stable. Characters of immature stages are described and compared to those of two other species in the genus.

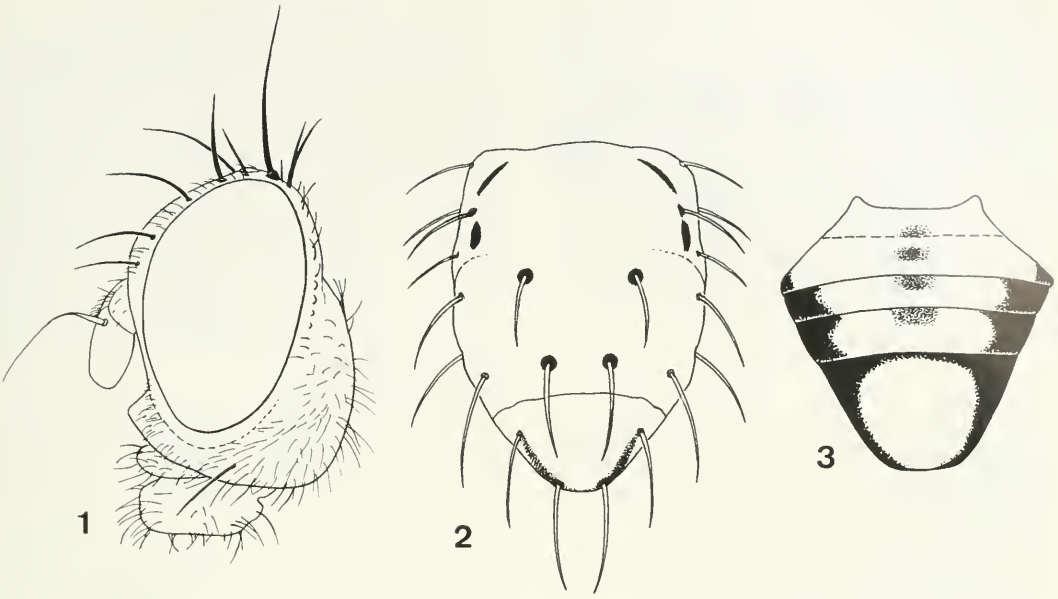
Key Words: *Craspedoxantha, C. yarivi* n. sp., fruit flies, phylogeny, *Vernonia*

Freidberg (1985) revised *Craspedoxantha* Bezzi (Tephritidae: Tephritinae: Terelliini) and included nine species. Freidberg and Mathis (1990) described a tenth species and analyzed the phylogenetic relationships within the genus using Hennig86© (see Fitzhugh 1989 for description). Their cladistic analysis resulted in two well-resolved trees (consistency index 86), comprising two well-supported species groups: the *marginalis* group, with four Afrotropical species (*marginalis* (Wiedemann), *milleri* Freidberg, *polyspila* Bezzi, *unimaculata* Bezzi); and the *manengubae* group, with four Afrotropical species (*bafut* Freidberg and Mathis, *manengubae* Speiser, *vernoniae* Freidberg, *yaromi* Freidberg) and two Oriental species (*indica* Zaka-ur-Rab, *octopunctata* Bezzi).

During two recent trips to the western Usambara Mountains, in northeastern Tanzania, Yariv Malihi and I collected and reared a new species of *Craspedoxantha* from its host plant, *Vernonia calvoana* ssp. *usambarensis* C. Jeffrey (Asteraceae: Vernonieae). Morphologically, this species of *Craspedoxantha* at first appeared to be intermediate between the two species groups of *Craspedoxantha*. It was therefore of interest to include it in a revised cladistic analysis and to see whether its addition would affect the overall phylogenetic picture. The new species is described below, and a cladistic analysis follows. Comments on two other species of *Craspedoxantha* are included.

MATERIALS AND METHODS

Adult flies were swept from host plants and reared from flower heads placed in organdy bags. Abdomens of some males and females were dissected, relaxed in 10% KOH, washed in water and preserved in glycerin inside microvials pinned with the specimens. While embedded in glycerine gel, the terminalia were studied and drawn, using a camera lucida. Puparial characters were studied and drawn in a similar manner. The procedures for the cladistic analysis are explained in the appropriate section below. Terminology follows Freidberg (1985) and Freidberg and Mathis (1986, 1990). The holotype and most other specimens are deposited in the entomological collection, De-



Figs. 1–3. Characters of *Craspedoxantha yarivi*. 1, Head, lateral view. 2, Thorax, dorsal view. 3, Abdomen, male, dorsal view.

partment of Zoology, Tel Aviv University (TAU).

Results

Craspedoxantha yarivi Freidberg, new species

(Figs. 1–13)

Diagnosis.—*Craspedoxantha yarivi* differs from all its congeners by the following unique combination of characters: Scutellum with black spots, and anepisternum with two setae (characters of the *marginalis* species group); femora not densely setulose ventrally, and dorsocentral seta aligned anterior of anterior supra-alar seta (characters of the *manengubae* species group). Other unique characters are blackish stripe bordering postpronotum dorsally (lacking in all other species), a distinct infuscation bordering crossvein dm-cu (lacking in all other species, except *C. milleri,* which has a more or less well defined crossband over this vein), and vein M ratio (ratio between apical and penultimate sections of this vein) about 1.5 (larger than 2 in all other species).

Description.—Specimens of this species were compared to the detailed generic description available for *Craspedoxantha* (Freidberg 1985). Discrepancies are noted below, accompanied by other characters considered significant. Specimens were brown in life. Chaetotaxy conforms with that of the genus and tribe (Freidberg 1985).

Head (Fig. 1): Head structure quite different from generic description and Fig. 1 of Freidberg (1985): Head relatively longer, with frons and frontofacial margin rounded, ventral facial margin strongly projecting and postgena more prominent; eye only about 1.6 times as high as long; face relatively low; antenna relatively short; 1st flagellomere 1.5 times as long as wide.

Thorax (Fig. 2): Presutural supra-alar seta aligned with anterior notopleural seta; dorsocentral seta aligned half way between anterior supra-alar seta and transverse suture; two anepisternal setae present. Scutal setulae fine, extending laterally to level of anterior supra-alar seta. Pattern of dark lateral spots on scutum and scutellum differs from all other species: anterior supra-alar

Fig. 4. Wing of *Craspedoxantha yarivi.*

spot lacking, 1 additional blackish microtomentose spot present, extending from anterior margin of scutum to presutural seta, bordering postpronotum dorsally; small blackish spot present around base of apical scutellar seta, sometimes extended to, or nearly to, base of basal scutellar seta and to tip of scutellum. Following spots similar to those of other species: presutural, 2 posterolateral spots (between wing base and scutellum), dorsocentral and acrostichal spots. Scutellum less convex, lacking blackish setulae, with sparse whitish setulae especially laterally; pleura mostly yellowish, with darker, rather inconspicuous longitudinal stripe at dorsal ⅓ of pleural region, extending from propleuron, which is usually with distinct small blackish spot (such spot lacking in other species), to anatergite, which is often also with small blackish spot; katepisternum similarly darker on ventral ⅔. *Legs:* Of elongate type (Freidberg 1985, Fig. 5); femora ventrally not densely setulose.

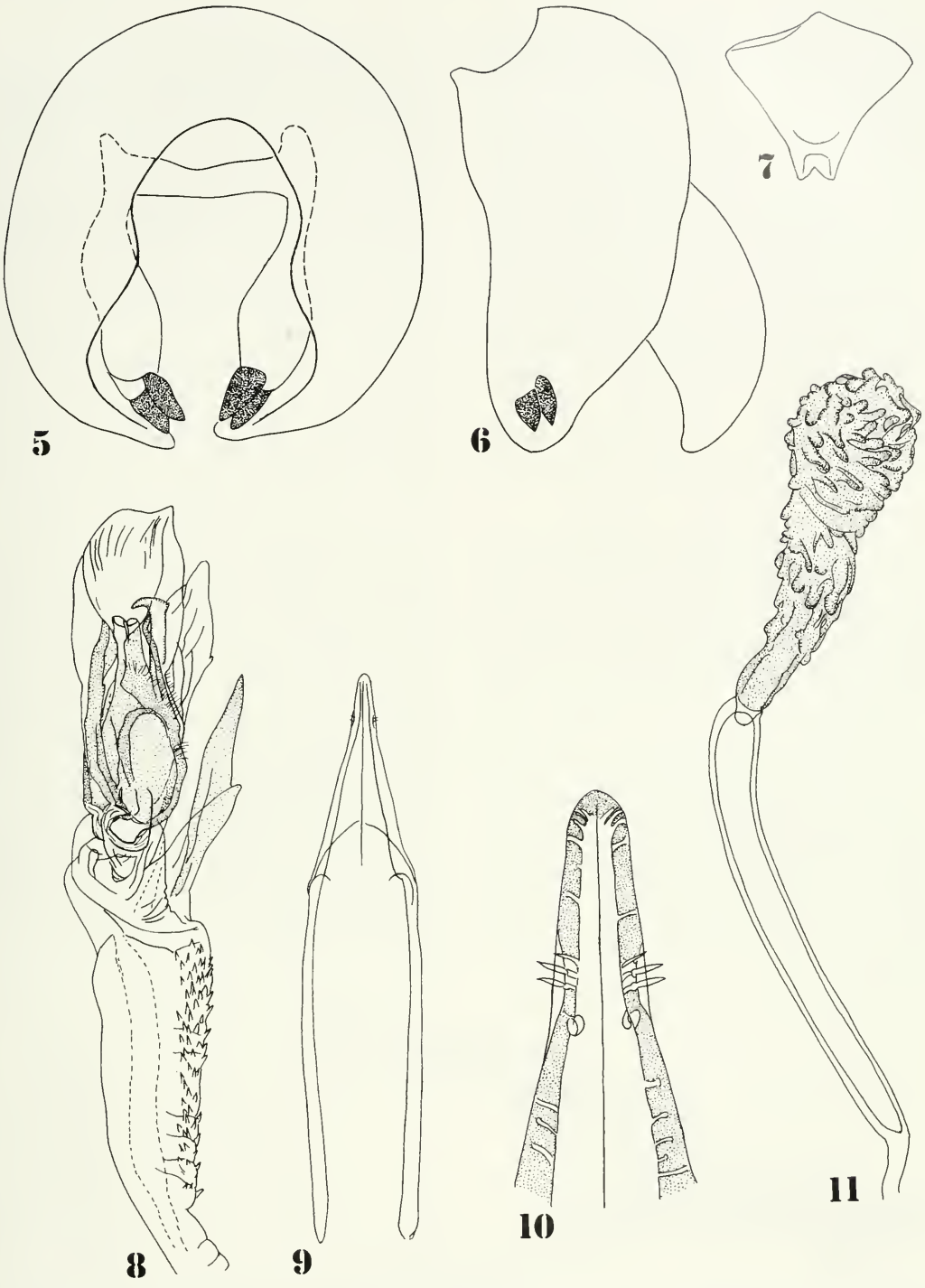
Wing (Fig. 4): Vein M ratio about 1.5; point of cell cup small; anterobasal part of wing hyaline, except small blackish spot at middle of cell c; marginal band extends from base of pterostigma and fork of veins R_{2+3} and R_{4+5} to slightly beyond end of vein M; crossvein dm-cu, including distal section of vein CuA_1, covered by distinct infuscate spot; posterior part of crossvein r-m also covered by infuscate spot; wing otherwise generally grayish. Length: 6–8 mm.

Abdomen (Fig. 3): Predominantly yellow, but with unique pattern in male: Syntergite 1+2 laterally with small blackish spot; T3 and T4 laterally with similar, though larger, spots; each of these tergites with additional small median spot; T5 with black, marginal, ring-shaped pattern, leaving greater central part and posteromesal margin yellow. Black pattern in female present or lacking; at maximum expression, syntergite 1+2 with rather large, median, triangular spot; T2 and T3 with small lateral spots; T3–T6 each with small median spot.

Terminalia (Figs. 5–11): Male: Epandrium rounded in posterior view (Fig. 5), with convex posterior margin in lateral view (Fig. 6); cerci triangular or diamond shaped (Fig. 7), sclerotized and bifurcate apically. Distiphallus (Fig. 8) with long tube spinose, preaedeagal swelling profusely spinulose, and otherwise rather similar to that of *C. vernoniae.* Female: Aculeus (Figs. 9–10) and spermatheca (Fig. 11) without overt features.

Material examined.—Holotype ♀: TANZANIA: Usambara Mts. [Mountains], Gologolo, 1,900 m, 23.viii.1996, A. Freidberg, ex flowerhead *Vernonia calvoana* ssp. *usambarensis,* ix. 1996. Paratypes: same collection data as holotype (36 ♂, 30 ♀); same data, but not reared (1 ♂, 7 ♀). Additional paratypes: TANZANIA: Usambara Mts., Rt. [Route] B124, Gologolo, 1,800 m, 12–13.ix.1992, A. Freidberg (2 ♂, 2 ♀); same data, but ex flowerhead *Vernonia calvoana* ssp. *usambarensis,* September 1992 (3 ♂, 3 ♀). The holotype is in excellent condition, pinned directly through the thorax, and is deposited in TAU. Paratypes will be distributed to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., The Natural History Museum, London, National Collection of Insects, Pretoria, and National Museum of Kenya, Nairobi.

Host plant, biology and immature stages.—The host plant, *Vernonia calvoana* ssp. *usambarensis* C. Jeffrey (Asteraceae: Vernonieae), was described from Lushoto District, Usambara Mountains, and is en-



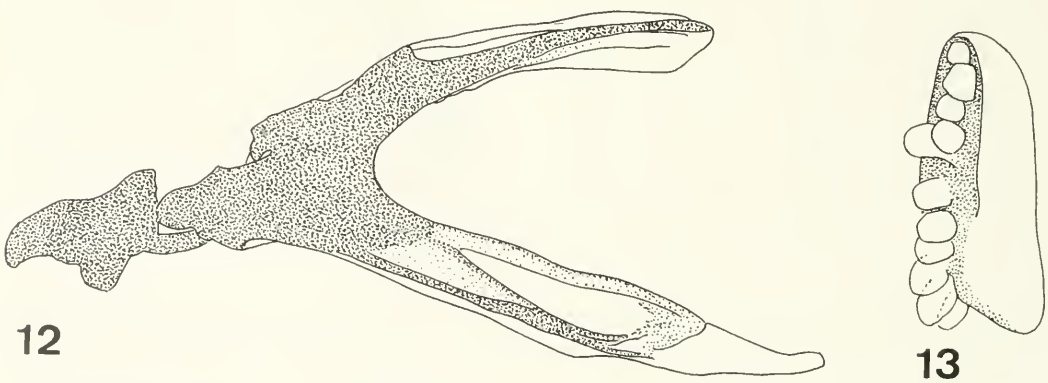
Figs. 5–11. *Craspedoxantha yarivi,* terminalia. 5, Epandrium, posterior view. 6, Epandrium, lateral view. 7, Cerci, male, posterior view. 8, Distiphallus. 9, Aculeus, whole. 10, Aculeus tip. 11, Spermatheca.

demic to Tanzania (Jeffrey 1988). It is the host of at least three additional species of tephritids, all apparently undescribed (Freidberg, unpublished observations). *Vernonia calvoana* (Hook. f.) Hook. f. is widely distributed over tropical Africa and consists of seven geographically more or less restricted subspecies (Jeffrey 1988). It was recorded as host of *C. vernoniae, C. yaromi* (Freidberg 1985), *C. bafut* and possibly *C. manengubae* (Freidberg and Mathis 1990), but the host subspecies were not indicated. Identification of the relevant host subspecies may show that speciation in some *Craspedoxantha* species may correspond to the level of subspecies of *V. calvoana.* The same pattern was also observed in some schistopterine tephritids infesting *V. calvoana* and other *Vernonia* Schreb. species (Freidberg, unpublished observations). Hence, if *C. yarivi* is indeed specific to the subspecies *usambarensis,* it may also be endemic to the same small geographical range of its host.

Adults of *C. yarivi* began to emerge from flower heads several days after the plants were collected and put in mesh bags, and emergence continued at least one week. Some puparia were found inside the bags, hence it is assumed that at least some maggots may usually leave the flower heads to pupate in the ground. These puparia formed the basis for the study of immature characters reported below.

A total of ten puparia were studied, some of them lacking parts of the operculum. The puparium is yellow, with distinct segmentation. Some puparia were entirely wrinkled, others were rather smooth, especially dorsally on the central segments. Wrinkles were circular, more or less parallel, somewhat irregular, with up to about 10 wrinkles on a single segment. Length: 4.75–6 mm (average: 5.6 mm); width: 2.3–3 mm (average: 2.75 mm). Cephalopharyngeal skeleton (Fig.12) about 0.9 mm long. Mandible without teeth, although concave (ventral) edge not entirely smooth, otherwise similar to that of *C. polyspila* and *C. marginalis* (Janzon 1985). Anterior spiracle (Fig. 13; N = 16) consisting of 9–11 digits (average 10; only 7 in *C. polyspila*), each 0.05–0.06 mm long. Digits, unlike in *C. polyspila,* are not arranged in a tight row. In unprepared puparia, digits appear to be 2–3 times longer than in the drawing, but this might be because the roots of the digits are visible under the surface of the cuticle. Posterior spiracle generally similar to that of *C. polyspila* but requires more careful study.

Etymology.—The species epithet, *yarivi,* is a genitive patronym in honor of my student, Mr. Yariv Malihi, who reared a large number of specimens, which comprise most of the type series.



Figs. 12–13. *Craspedoxantha yarivi,* puparium. 12, Cephalopharyngeal skeleton. 13, Anterior spiracle.

Craspedoxantha bafut Freidberg and Mathis

Craspedoxantha bafut Freidberg and Mathis 1990: 325.

This species was described from Cameroon and Nigeria based on 13 specimens, some of them reared, and has not been recorded subsequently. A recent checking of the type material revealed that the holotype (Cameroon, Rt. N6, Bali-Batibo, W. of Bamenda, 20.xi.1987, A. Freidberg, deposited in TAU) is a male, not a female, as stated in the original description.

Craspedoxantha milleri Freidberg

Craspedoxantha milleri Freidberg 1985: 195.

This species was described based on a single male collected on the Drakensberg, Natal, South Africa. A second male from the same general region is now available for study. It is labeled: Blue Mountain Pass, Makhaleng Valley, Maloti Mountains, 2,150–2,525 m, 12–14 Jan. 1963. Another label: Maseru District, Basutoland, B. & P. Stuckenberg (National Collection of Insects, Pretoria). This specimen fits the original description well, except that it is smaller than the male holotype (only 4.5 mm, instead of 5 mm), and the transverse band over the crossveins is narrower and interrupted, especially over vein M. The epandrium has a concave posterior margin in lateral view (not studied in the holotype).

Cladistic analysis of *Craspedoxantha*

For a detailed explanation of the cladistic methodology and its application to *Craspedoxantha,* see Freidberg and Mathis (1990). Trees were calculated from the character data using the "implicit enumeration" option of Hennig86. The only differences from the character matrix of Freidberg and Mathis (1990) are the addition of *Craspedoxantha yarivi* (the new species) and *Chaetostomella cylindrica* Robineau-Desvoidy (as a second outgroup), and some changes, mostly additions, to the characters used in the analysis. A brief presentation of the 13 characters used in the analysis and coding of the character states are given below. The character matrix is in Table 1. All characters with three character states were coded "additive."

Table 1. Character matrix for species of *Craspedoxantha* and two outgroup species.

Taxon	0000000001111 1234567890123 (Characters)
Orellia punctata	0000000000000
Chaetostomella cylindrica	0010000010100
Craspedoxantha bafut	1211110211001
Craspedoxantha indica	0211110100000
Craspedoxantha manengubae	1211110212001
Craspedoxantha marginalis	0100011200001
Craspedoxantha milleri	0000011000002
Craspedoxantha octopunctata	0201110100002
Craspedoxantha polyspila	0000011210000
Craspedoxantha unimaculata	0100011202002
Craspedoxantha vernoniae	1211110112011
Craspedoxantha yarivi	0110000212121
Craspedoxantha yaromi	1211100111001

Thorax

1. Size of presutural black spots: about as large as dorsocentral spots (0); distinctly smaller than dorsocentral spots (1).
2. Number of black spots on scutellum: 3–4 (0); 2 (1); 0 (2).
3. Alignment of dorsocentral seta: with anterior supra-alar seta (0); distinctly anterad of anterior supra-alar seta (1).
4. Number of anepisternal setae: 2 (0); 1 (1).
5. Lateral extension of scutal setulae: to level of anterior supra-alar seta (0); to level of presutural seta (1).
6. Coloration of scutellar setulae: all or most setulae yellow (0); all or most setulae black (1).

Legs

7. Structure and vestiture of femora: slender and lacking dense investment of setulae (0); swollen and densely setulose ventrally (1).

Table 2. Character analysis for species of *Craspedoxantha* and two outgroup species.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13
Steps	2	4	2	2	2	3	1	5	3	2	2	2	2
Consistency index	50	50	50	50	50	33	100	40	33	100	50	100	50
Retention index	66	75	80	80	80	33	100	57	60	100	0	100	66

Wing

8. Additional band or spot present over crossvein dm-cu and connected or disconnected to marginal band (0); such band or spot lacking, but marginal band approaching crossvein r-m (1); such band or spot lacking, and marginal band not approaching crossvein r-m (2).
9. Color of cell cup: distinctly yellow (0); indistinctly yellow (1).

Abdomen

10. Shape of posterior margin of the epandrium (the surface from which the cerci arise) in lateral view: concave (0); straight (1); convex (2).
11. Long tube of distiphallus: not spinose (0); spinose (1).
12. Preaedeagal swelling: not spinulose (0); slightly spinulose (1); profusely spinulose (2).

Biology

13. Host plants: Host plant associations that are in part or exclusively with-*Vernonia* Schreb. (tribe Vernonieae) are hypothesized as the derived condition (1). I was unable to hypothesize a complete transformation series for the other host associations, whether they include plants of the tribe Cardueae (hosts of most Terelliini), Lactuceae (host of *Orellia* Robineau-Desvoidy species) or others, and I therefore coded them all as primitive (0).

The results of the cladistic analysis are presented below (Fig. 14), and the analysis of the characters is given in Table 2.

Discussion

The main purpose of this study was to describe a new species of *Craspedoxantha* and to revise the phylogeny of this genus. The new species, *C. yarivi,* possesses most adult characters of this rather homogenous genus. By its morphology, it appears to be an intermediate species between the two previously recognized species groups. However, in the cladistic analysis above, it appears as a terminal clade of the *manangubae* group, not upsetting the basic division into the two species groups, rather supporting it. Yet, the monophyly of these species groups is now primarily substantiated by two characters (the alignment of the dorsocentral setae and the structure and vestiture of the femora), rather than the four characters that were available before *C. yarivi* was discovered (Freidberg 1985).

In the cladistic analysis I first used the "implicit enumeration" option. Six trees resulted from this option, but only one (Fig. 14) was similar to the Nelson consensus tree of Freidberg and Mathis (1990: fig. 5) in supporting the same (*marginalis* and *manengubae*) species groups. Two of the other trees did not support any species grouping, and the other three trees progressively supported a stronger *marginalis* group, culminating with a resolved group containing *C. marginalis, C. unimaculata* and *C. polyspila.* However, in all these five trees *C. milleri* branched at the base, forming an outgroup to all other species of *Craspedoxantha.* The successive weighting technique was then used, resulting in one tree that is identical to the above mentioned tree (Fig. 14) of the "implicite numeration" option. This tree is fully resolved and includes *C. yarivi* as the sister species of *C. vernoniae* in the *manengubae* group.

Two noteworthy autapomorphies of *C. yarivi* are the completely whitish-setulose scutellum and the infuscated spot on crossvein dm-cu. Blackish setulae on the scutel-

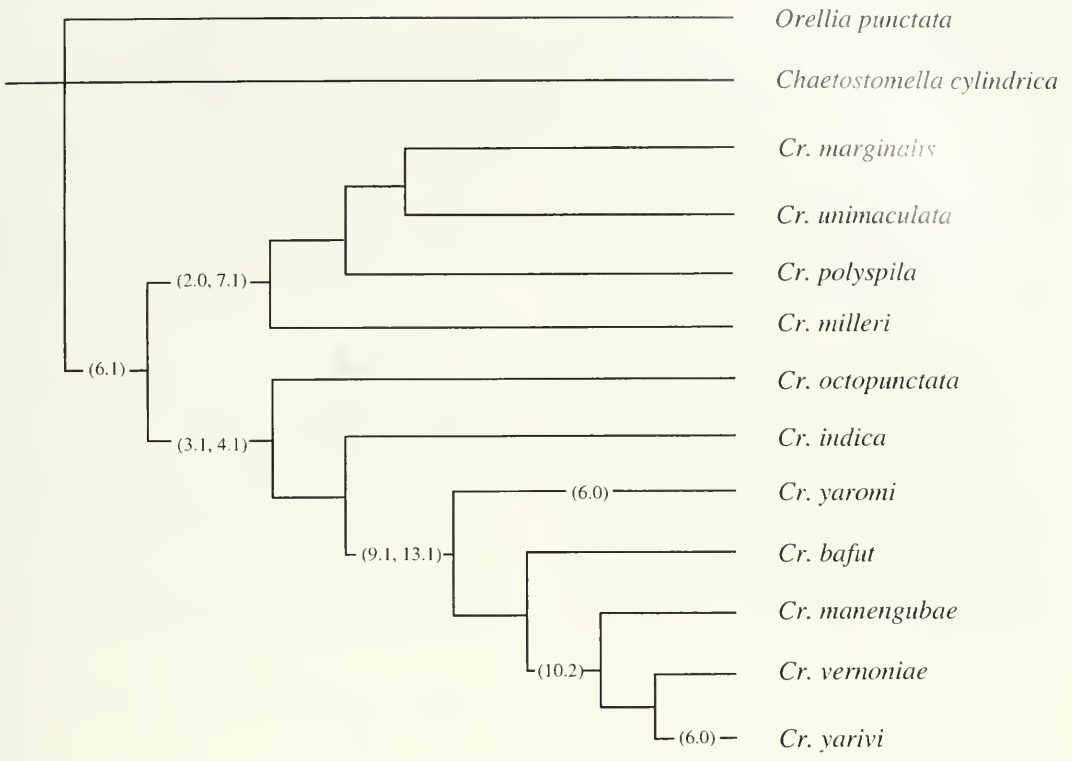


Fig. 14. Reconstructed phylogeny for species of *Craspedoxantha* and two outgroup species. Character numbers refer to the cladistic section.

lum were one of the main diagnostic characters of *Craspedoxantha* (see key to terelliine genera in Freidberg 1985), and the entirely whitish setulae on the scutellum of *C. yarivi* renders the monophyly of this genus less substantiated. The second noteworthy apomorphy, viz. an infuscated spot restricted to crossvein dm-cu, is unique to *C. yarivi,* although a similar character is found in *C. milleri,* in which a cross band near the middle of the wing extends over both crossveins r-m and dm-cu (Freidberg 1985).

The monophyly of *Craspedoxantha* is now supported by only two unequivocal characters: the relatively high eye (1.5–2 times as high as long) and the uninterrupted yellow costal band on the wing (spotted with black). The monophyly of the genus may also be supported by zoogeography, as *Craspedoxantha* is the only tropical genus of Terelliini, and it is disjunct or nearly disjunct from the other terelliine genera (which are essentially Palearctic and/or Nearctic). I suggest continuing to treat *Craspedoxantha* as a valid genus at least until this validity is tested by a cladistic analysis of the entire tribe.

The comparison between puparial characters of *C. yarivi* and larval characters of *C. polyspila* and *C. marginalis* (Janzon 1985) indicated that characters of immature stages may be significant for the classification of *Craspedoxantha.* Some differences in the shape of the cephalopharyngeal skeleton and anterior spiracles were noted. These differences may represent supraspecific categories. However, additional species should be studied before this assumption can be substantiated.

Additional new species of *Craspedoxantha* should be expected in Africa, and perhaps also in southeast Asia, especially if all subspecies of *Vernonia calvoana* and

other *Vernonia* species are searched for these flies.

Acknowledgments

I am grateful to my student, Yariv Malihi, who diligently helped me during a recent collecting trip to Tanzania, especially in rearing the large series of specimens that formed the basis to this paper. I am also grateful to Wayne N. Mathis (Smithsonian Institution) and Allen L. Norrbom (Systematic Entomology Laboratory, USDA, % Smithsonian Institution) for their help and useful suggestions, to Bernhard Merz, ETH, Zurich, for reviewing a final draft of the manuscript, to Fini Kaplan, for continuous encouragement, to Walter Ferguson for the drawings and to Amikam Shoub for the photograph.

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A NEW GENUS *CLYPEOLONTHA* LI AND YANG, FOR THE GENUS *MELOLONTHA* FABRICIUS (COLEOPTERA: SCARABAEOIDEA: MELOLONTHINAE) FROM SOUTHEASTERN ASIA

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Abstract.—***Clypeolontha,*** new genus, is described with *Melolontha alboplagiata* Brenske, **new combination,** as the type species. In addition, three species are herein recognized as new: ***C. siamensis, C. bertiae,*** and ***C. laosensis.*** The following information is provided for each species, when appropriate: literature review, diagnosis, description or redescription, illustration of important external characters, data for material studied, geographical distribution, and taxonomic remarks. A key to females and a distribution map to the *Clypeolontha* species are given. A preliminary discussion on the systematics of *Melolontha sensu lato* is presented.

Key Words: Melolonthinae, *Melolontha, Clypeolontha,* new genus

As the type genus of the subfamily Melolonthinae, *Melolontha* Fabricius, 1775, has attracted attention because of their diversity and agricultural importance of its species. Burmeister (1855) first treated this genus and assigned *Hoplosternus* Guérin-Méneville, 1838 and the newly defined *Schoenherria* as members of *Melolontha,* although both are later widely accepted as independent genera. Reitter (1902) proposed four groups mainly based on their geographical distributions in his division of *Melolontha,* including *Tocama,* the first subgenus from mainland China. Medvedev (1951) designated the second subgenus, *Apropyga,* under a strict concept of *Melolontha* in his faunal review.

Since these beetles are widely distributed throughout Eurasia, it is surprising that no revision encompassing the some 40 constituent species within *Melolontha* has ever been furnished to date. Most taxonomic works for *Melolontha* consist of isolated contributions. Medvedev (1951) is probably the most comprehensive study so far, particularly his subgeneric treatment, which includes all species of *Melolontha* from the former Soviet Union and adjacent regions. Nomura (1952) reviewed the northeastern Asian *Melolontha* species and described a related genus, *Tricholontha,* endemic to the Okinawa Islands, Japan. Baraud (1992) provided a identification key as well as a detailed literature review for each of the nine nominal European species of *Melolontha.* Neither of these works discussed the systematic problems of *Melolontha.*

Since the first *Melolontha* was described, several species have been removed, or established as the type species of new genera and more cases will likely be reappraised in the future. Apparently, the broad concept of *Melolontha* is a result of all allied genera being lumped together. Not only do they all share the common character of a 7-segmented antennal club, but sometimes, particularly at the earlier taxonomic works, merely an enlarged antennal club. The type

species of the genus *Cyphochilus* Waterhouse, 1867, *C. candidus* (Olivier 1789), is an obvious example with a 3-segmented enlarged club in males and previously considered a *Melolontha*. Thus, a reasonable classification system within the whole subtribe Melolonthina also needs further construction and analysis. Most recently, Baraud (1992) provided two other diagnostic characters, namely the membranous margin of the elytra and the number of antennal club segments in females, to seperate *Melolontha* from *Polyphylla* Harris, 1941. These two characters and the ratio between eye and interocular width used by Nomura (1952) are characters (in addition to male antennal segments) employed to distinguish *Melolontha* from other related taxa.

In fact, most of those genera closely related to *Melolontha* (i.e., *Polyphylla* Harris, *Schoenherria* Burmeister, 1855 and *Exolontha* Reitter, 1901) are most diverse and are mainly distributed in or restricted to East and Southeast Asia. However, we will provide further information with broad evolutionary implications to those, described or undescribed, taxa closely related with *Melolontha sensu lato* which based on cladistic analysis within the next complementary work and this is the first part we refer to the taxonomic assessment of *Melolontha sensu lato* (see also Systematics).

Material and Methods

Specimens used in this study were borrowed from and deposited in the institutions referred to in the section of material or type. The acronyms follow Arnett et al. (1993) and are listed below.

BMNH: The Natural History Museum, London, U.K.; Malcolm Kerley.

ISNB: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; Konjev Desender and Marcel Cludts.

MNHA: Museum of Nature and Human Activities, Hyôgo, Japan; Yoshihisa Sawada.

MNHN: Muséum national d'Histoire naturelle, Paris, France; Jean J. Menier and Nicole Berti.

NMNH: National Museum of Natural History, Taichung, Taiwan; Mei-Ling Chan.

NTUI: Insect Museum, Department of Entomology, National Taiwan University, Taipei, Taiwan; Tung-Ching Hsu.

TARI: Taiwan Agricultural Research Institute, Taichung, Taiwan; Liang-Yih Chou.

ZMNB: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; Hella Wendt and Joachim Schulze.

Observation and measurements of external characters were made using an ocular micrometer. Male genitalia were dissected and cleaned using 10% KOH solution for few days, then stored in glycerine in microvials and attached to specimens from which they have been removed.

The specimen label data has been abbreviated to indicate as a handwritten (H) or a printed (P) data respectively. Separate labels are indicated by double slashes from another while specimens with two more ones. The information on geographical distribution is referred from label data.

The measurements and ratios that are considered to be useful in the separation of *Clypeolontha* species are briefly summarized in Table 1. Abbreviations for characters and mensural procedures are listed as follows:

BL body length, measured from anterior margin of clypeus to the apex of elytra.

BW body width, measured across elytral humeri.

BW/HW ratio of body width to head width across eyes in female.

MPR ratio of maximum length of female maxillary palpi 2–4.

ASR ratio of length of male antennal basal segments 1–3.

Table 1. Summary of selected descriptive measurements and ratios for species of *Clypeolontha*: range, mean and standard deviation.

Taxa (n)	Body length (BL), mm	Body width (BW), mm	BL/BW	MFL/W	PgW/L
C. siamensis	16.4–19.6	8.0–9.0	2.05–2.21	2.93–3.21	1.08–1.22
Male (21)	18.4 (0.84)	8.65 (0.31)	2.13 (0.06)	3.06 (0.06)	1.15 (0.38)
Ditto, female (8)	19.7–20.7	9.3–10.0	2.04–2.17	2.34–2.56	1.17–1.25
	20.2 (0.22)	9.6 (0.32)	2.09 (0.05)	2.45 (0.08)	1.21 (0.06)
C. alboplagiata	16.8–17.0	7.8–8.0	2.13–2.15	2.42–2.50	1.00–1.03
Male (4)	16.9 (0.1)	7.9 (0.1)	2.14 (0.01)	2.46 (0.04)	1.02 (0.02)
Ditto, female (3)	19.8–20.1	8.8–9.0	2.23–2.25	2.08–2.18	1.11–1.14
	19.95 (0.15)	8.9 (0.1)	2.24 (0.01)	2.13 (0.05)	1.125 (0.01)
C. bertiae (5)	17.9–18.5	7.8–7.9	2.28–2.36	2.34–2.45 (n = 4)	1.08–1.12
	18.2 (0.3)	7.9 (0.06)	2.36 (0.01)	2.40 (0.08)	1.10 (0.02)
C. laosensis (1)	17.2	7.5	2.29	2.61	1.18

PTR ratio of maximum length of protarsomeres 1–5.

MFL/W ratio of length of metafemur to its maximum width in ventral aspect.

PgW/H ratio of height of pygidium to its maximum width in dorsal aspect.

Systematics

The taxonomic legacy surrounding the members of the genus *Melolontha sensu lato* has sufferred many changes in position. These situations may become more complicated as more new taxa are discovered. We consider that the lack of systematic research related to the genera of *Melolontha*, especially *Hoplosternus,* and lack of taxonomic characters that clearly delimit all closely related genera, are apparently the reasons for confusion regarding the classification of melolonthine taxa. Since we recently acquired many related taxa from various geographical areas and the senior author has seen many types and other specimens from several European institutions, it was felt time is appropriate to make a new definition of *Melolontha.* Therefore, the establishment of new genus *Clypeolontha* is herein proposed to accommodate those questionable taxa, in part, presently assigned to *Melolontha sensu stricto.* Several other taxa are also in need of a reassessment in their taxonomic placement but will be discussed at a later date.

Through examinations of 25 of 41 currently valid species in *Melolontha* and 20 of 29 species in *Hoplosternus,* we present the following diagnostic characters, based mainly on the type species, *Melolontha melolontha* L. for *Melolontha sensu lato:* (1) presence of metallic coppery with some green or purple coloration on head, pronotum, scutellum and femora when surface setae are removed; (2) overall punctation of pronotum usually coarser and sparser with varied distribution; (3) each elytron with 5 discal costae including 1 along epipleural margin; (4) lateral sides of abdominal sterna 1–6 usually with a lighter maculation, although on sternite 6 sometimes less developed; and (5) male genitalia in general symmetrical, apex of parameres usually obliquely truncate and swollen when viewed laterally, in frontal aspect with trapezoid to broad bean-like swelling, dorsal portion with hook apically. In the time past, *Melolontha* and *Hoplosternus* were differentiated based only on the appearance and development of mesosternal process. Arrow (1913) first argued against this character when he wrote that the male of *M. guttigera* Sharp lack the mesosternal process while the female has one. However, we have examined many determined specimens of *M. guttigera* and found that both sexes did

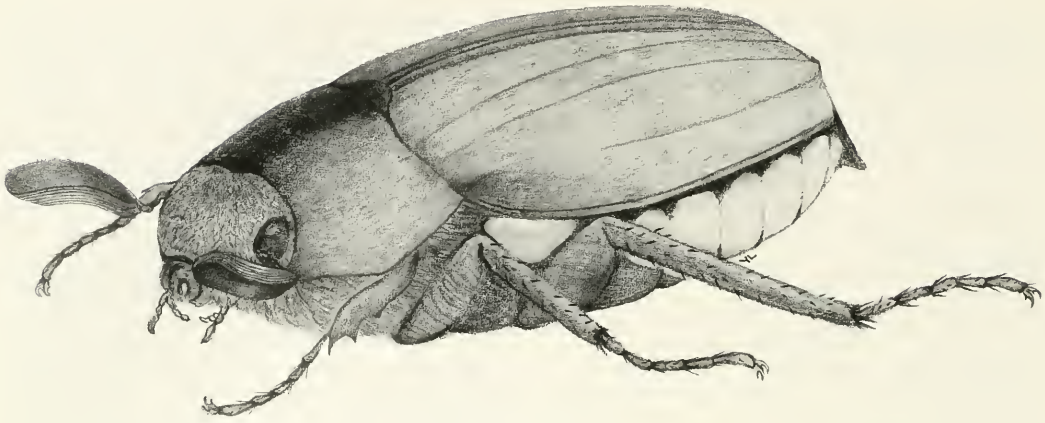


Fig. 1. *Clypeolontha siamensis*.

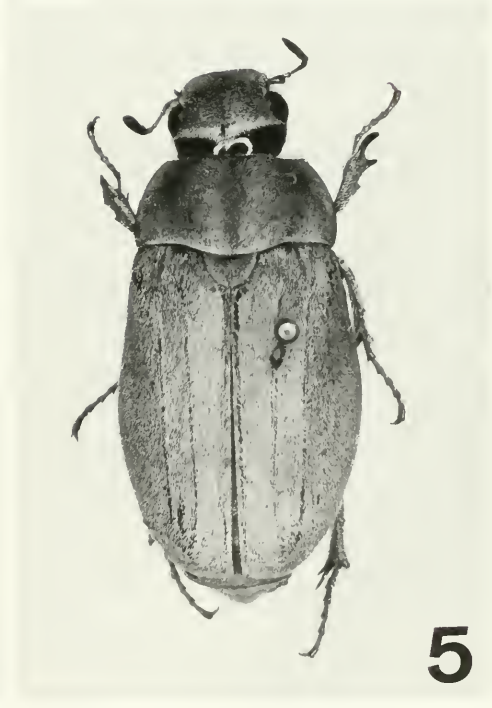
have the mesosternal process although the male has a remarkably less-developed one than female. Regardless, it is our view that the genus *Melolontha* is probably paraphyletic when *Hoplosternus* is treated as an independent derivative from *Melolontha*. The only distinctive character, the mesosternal process, used to separate *Hoplosternus* from the other taxa is subject to a broad transitional intra/inter-specific variation, and it is also commonly found in many genera of Scarabaeidae. Thus, this character, a plesiomorphic feature, is useless for recognition of *Hoplosternus* as an independent genus and we will present a formal taxonomic treatment in the future. Furthermore, as will be proposed cladistically elsewhere (Li in preparation), members of the true *Melolontha* lineage are defined by the above-mentioned synapomorphies (1), (2), (4), and (5). All of these characters are shared by *Melolontha* and *Hoplosternus*. It is unlikely that these structures evolved twice because they are found in the same geographical distributions of Eurasia with a sympatric distribution pattern and have not been discovered elsewhere.

Brenske (1898) described *M. alboplagiata* (here referred to as *Clypeolontha*), based only on a single female specimen. Even lacking a male, Brenske still assigned this species to a member of *Melolontha* probably because its wide maculation continuously located along the lateral sides of abdominal sternites 1–6 makes it morphologically closed to *Melolontha* than the other genera. However, this character is not shared by *Melolontha* and is one of autapomorphic characters defining our new genus. Fortunately, we obtained a series of both sexes collected from the type locality and neighboring areas. These were compared with the type and other related taxa from Southeast Asia respectively. Therefore, we here propose the new genus, *Clypeolontha* for *M. alboplagiata* together with three other new species.

Clypeolontha Li and Yang, new genus

Type species. *Melolontha alboplagiata* Brenske 1898: 236, here designated.

Diagnosis.—The following combination of characters separate *Clypeolontha* from all other related genera within the subtribe Melolonthina. Body oblong, subparallel-sided medially, smaller (16.4–19.6 mm), and absence of metallic coloration or reflection on body surface, antennae, and legs. Head surface densely rugose, clypeus shallowly depressed, emarginate centrally exposing labrum when viewed dorsally. Pronotal surface densely punctate, punctures evenly distributed, each with a seta subequal in length, lateral margins very weakly and incompletely serrate; pro- and mesosternal processes vestigial. Pretarsus



Figs. 2–5. Dorsal habitus. 2, *Clypeolontha siamensis,* holotype male. 3, *C. alboplagiata,* male. 4, *C. siamensis,* female. 5, *C. alboplagiata,* holotype female.

small, subapical tooth one-half to two-thirds length of apical claw. Metepisternum and metepimeron densely covered with scales. Six visible abdominal sternites with lateral maculation on ventrites 1 through 6, narrowest on ventrite 1, expanding obliquely towards middle through to about ventrite 4 and decreasing 5 in width through to 6, which maculation consisting of dense white scales with faint iridescent-tinged reflection continuous throughout the lateral edges. Paramere of male genitalia asymmetrical.

Etymology.—The prefix of the generic name is derived from the Latin combining form *clypeo-*, reflecting distinctive character of clypeus on both sexes among species, and the suffix is partly taken from the genus *Melolontha* showing their close relationship. The gender is feminine.

Key to Females of *Clypeolontha*

The key is based on females only; males material were not available for two species in this study. However, we consider that the distinguishing characters employed herein are constant throughout each species. Additionally, we provide a diagnosis to the species with male specimens compared.

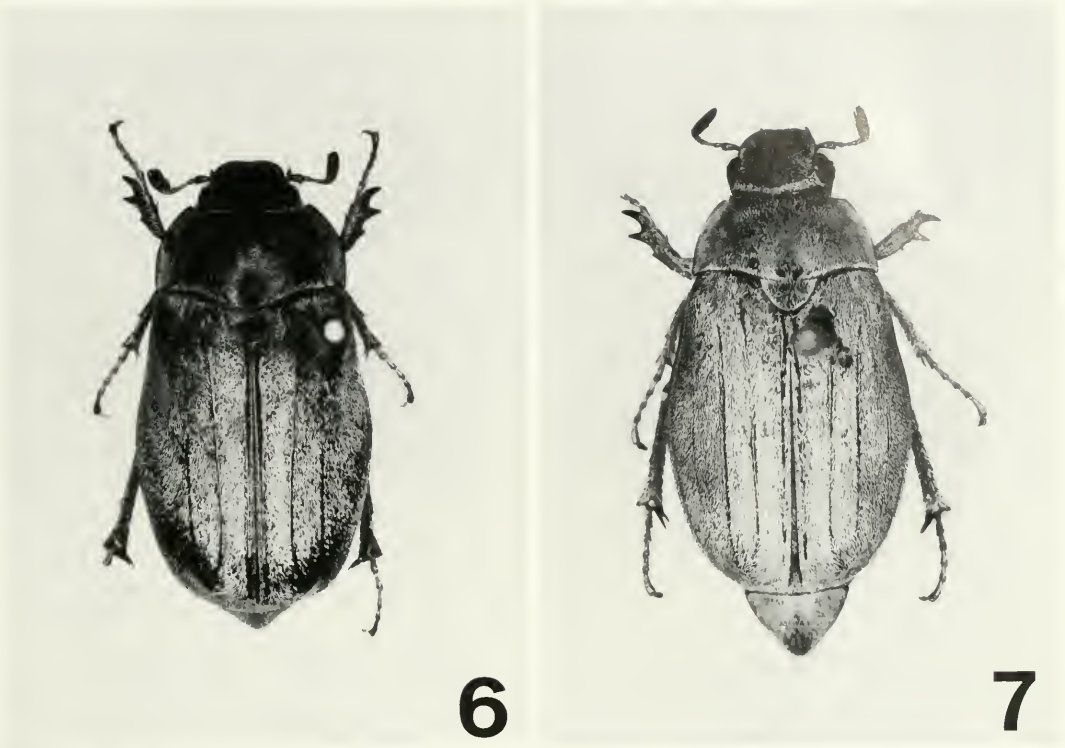
1. Body size larger (BL ≧ 19.7 mm, BW ≧ 8.8 mm, BL/BW ≦ 2.25; surface usually clothed with yellowish-brown to whitish-yellow setae . . 2
– Body size smaller; pronotal and elytral surfaces clothed with pale white to yellow setae 3
2. Labrum triangular (Fig. 11); apical maxillary palpomere spindly elongate, longer than combined segments 2–3 (Fig. 43) (mean MPR = 1.6:1.3:3.7); pronotal midline not visible, angles obtuse (Fig. 13); mean BW/HW = 1.64; hind femur broadly stout (Fig. 19) (MFL/W = 2.08–2.18); abdominal sternite 5 with posterior edge smooth (Fig. 25); apex of pygidium somewhat sharpened (Fig. 31); PgW/H = 1.11–1.14; Sikkim and Bhutan . . . . . *C. alboplagiata* Brenske
– Labrum rounded (Fig. 10); apical maxillary palpomere elongate, bulged centrally, subequal to combined segments 2–3 (Fig. 42) (mean MPR = 1.9:1.4:3.5); pronotal midline shallowly depressed, angles acute (Fig. 12); mean BW/HW = 1.84; hind femur stout (Fig. 17) (MFL/W = 2.34–2.56); abdominal sternites 5 and 6 anteriorly point-curved medially (Fig. 25); pygidium broadened basally with apex rounded and inflated (Fig. 29); PgW/H = 1.17–1.25; northern Thailand . . . . . *C. siamensis*, n. sp.
3. Clypeus very shallowly depressed anteriorly; apical maxillary palpomere spindly elongate, equal to combined length of segments 2–3 (Fig. 44) (mean MPR = 2.0:1.5:3.5); pronotal disc moderately convex with finely punctate, evenly distributed, midline not visible, angles weakly protuberant (Fig. 14); mean BW/HW = 1.73; protibial spur subequal to one-fourth length of first pretarsomere; hind femur roundly inflated (Fig. 20) (MFL/W = 2.34–2.45); posterior edges of abdominal sternites 5 and 6 smooth, sternite 6 with feeble irregular serration (Fig. 26); pygidium clothed with pale white to yellowish-brown setae, moderately elongate with apex sharpened (Fig. 32); PgW/H = 1.08–1.12; western Laos and northeastern Thailand . . . . . *C. bertiae*, n. sp.
– Clypeus moderately depressed anteriorly; apical maxillary palpomere spindly stout, shorter than combined length of segments 2–3 (Fig. 45) (MPR = 1.8:1.3:2.7); pronotal disc weakly convex with irregularly distributed punctures, midline shallowly depressed, bearing tiny brownish setae, anterior angle acute, posterior angles obstuse (Fig. 15); BW/HW = 1.91; protibial spur subequal to one-third length of first pretarsomere; hind femur slightly transversely inflated (Fig. 21) (MFL/W = 2.61); posterior edge of abdominal sternite 5 distinctly point-curved, sternite 6 strongly arc-curved medially (Fig. 27); pygidium clothed with yellowish brown setae, slightly elongate with apex rounded (Fig. 33); PgW/H = 1.18; central northeastern Laos . . . . . *C. laosensis*, n. sp.

Clypeolontha siamensis Li and Yang, new species

(Figs. 1, 2, 4, 8, 10, 12, 16, 17, 22, 25, 28, 29, 34, 35, 36, 37, 42)

Melolontha alboplagiata Brenske: *sensu* Itoh 1995: 202 (distribution, new record).

Type series.—Holotype ♂ (deposited in NTUI as DPPE-9702): N. THAILAND: Chiang Mai Prov., Fang, 9.V.1995. Paratypes (18 ♂, 7 ♀) as follows: same data as holotype: 9 ♂, 4 ♀; 1 ♂, 25.IV.1995; the remaining 6 ♂ and 2 ♀, Chiang Rai Prov., Wiang Pa Pao, all on 1.V.1995 but 1 ♂ on 5.IV.1995 (2 ♂ paratypes deposited in BMNH; 2 ♂ in TARI; 3 ♂ and 2 ♀ in NMNH; 3 ♂ and 2 ♀ in ZMHB; 3 ♂ in



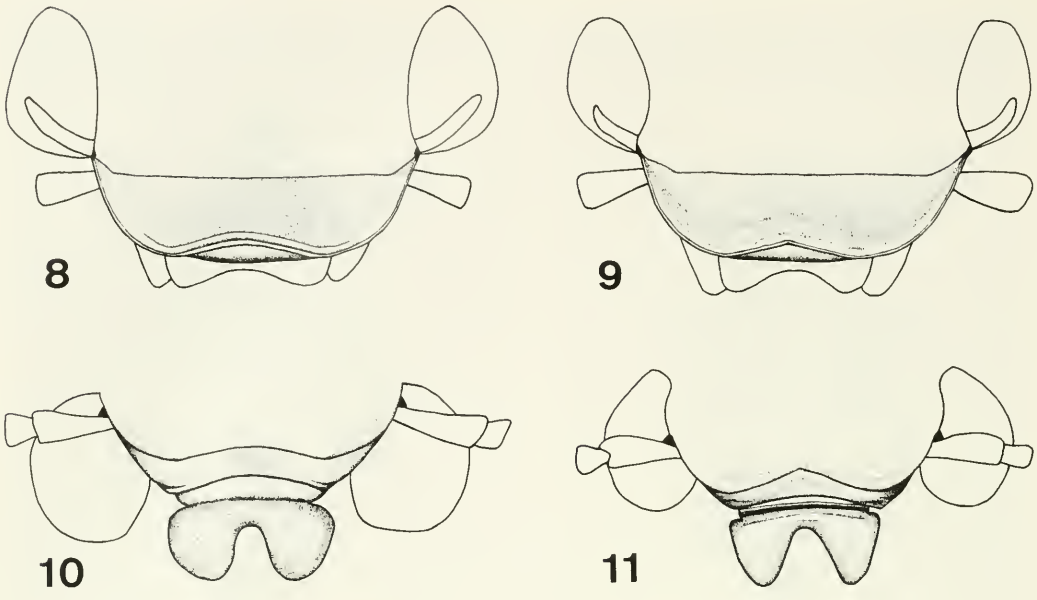
Figs. 6–7. Dorsal habitus. 6, *Clypeolontha laosnesis*, holotype female. 7, *C. bertiae*, holotype female.

ISNB); 1 ♂ dated May 27, 1990 from Wiang Papso, N. Thailand and 1 ♀ dated May 1, 1988 from Samoeng, near Chiang Mai, N. Thailand in Takeshi Itoh's collections; 1 ♂ dated May 10–13 from Doi Song, near Chiang Mai in MNHA The remaining paratypes, 3 ♂ and 2 ♀ are deposited in NTUI and the authors' collections, respectively.

Male diagnosis.—Antennal club 2.3–2.7 times length of stem; mean ASR = 2.1:0.7:1.3; labrum shape rounded; pronotal midline very shallowly depressed, angles acute; protarsomere 1 shorter than combined length of protarsomeres 2 and 3 (PTR = 3.0:1.7:1.6:1.6:2.7); hind femur stout (MFL/W = 2.93–3.21); abdominal sternite 5 with posterior edge moderately arc-shaped centrally; apex of pygidium distinctly prolonged, longitudinally convex, PgW/H = 1.08–1.22; paramere apex irregularly broadened, right paramere with a inward spine on basal one-fourth.

Description.—Male. *Body:* Oblong (Figs. 1, 2), sides subparallel medially. Dorsal surface densely covering with short yellowish-brown to whitish-yellow setae, same in length. BL = 16.4–19.6 mm; BW = 8.0–9.0 mm; BL/BW = 2.05–2.21. Basal color blackish brown to yellowish brown.

Head: Surface densely to confluently punctate, punctures moderately large, each bearing a short seta. Antenna 10-segmented with 7-segmented club; lamellae slightly outwardly curved, 2.3–2.7 times length of stem; first basal segment wider than third one; mean ASR = 2.1:0.7:1.3. Clypeus transverse, shallowly depressed anteriorly, weakly emarginated; sides gradually rounding to biarcuate apex; middle of anterior margin shallow and smooth (Fig. 8); clypeo-frontal suture moderately developed; frons slightly narrowed, making eyes large. Labrum weakly to moderately grooved with respect to clypeus; transversally symmetrical, rounded and strongly bilobed, one-third



Figs. 8–11. Labrum. 8, *Clypeolontha siamensis*, dorsal view. 9, *C. alboplagiata*, dorsal view. 10, *C. siamensis*, front view. 11, *C. alboplatiata*, front view. Scale line = 2.0 mm.

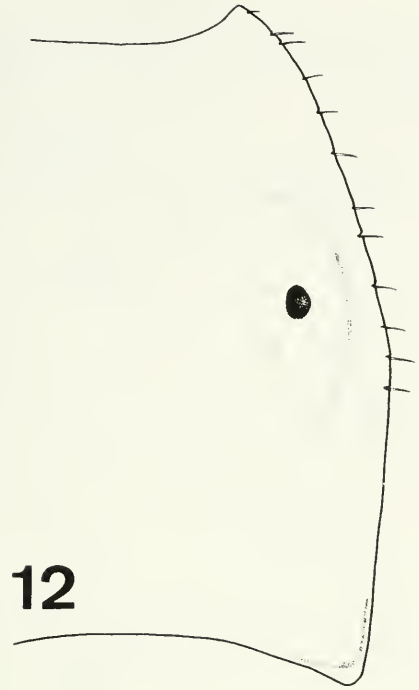
width of clypeal base, depressed laterally (Fig. 10); visible dorsally, moderately protuberant. Maxillary palpus light yellowish brown, 4-segmented; apical palpomere spindly elongate, truncate, centrally bulged, longer than combined length of palpomeres 2–3, each with a dorsal concavity. Labial palpus 3-segmented; apical palpomere subcylindrical and glabrous.

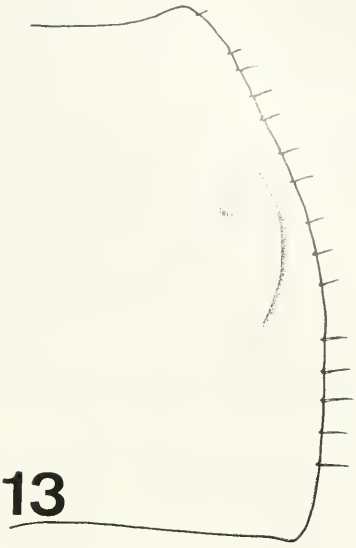
Pronotum: Moderately transverse to subquadrate, widest at middle, slightly narrowing posteriorly, weakly convex. Surface densely punctate, punctures evenly distributed, each with a short seta; anterior margin weakly emarginate. Midline very shallowly depressed and always covered with less stout and somewhat shorter setae than lateral. Discal sides of pronotum irregularly convex at middle, each with a varied pit (Fig. 12). Laterally, marginal serration poorly developed; both anterior and posterior angles acute, moderately protuberant (Fig. 12). Scutellum wider than long, apically rounded, moderate in size.

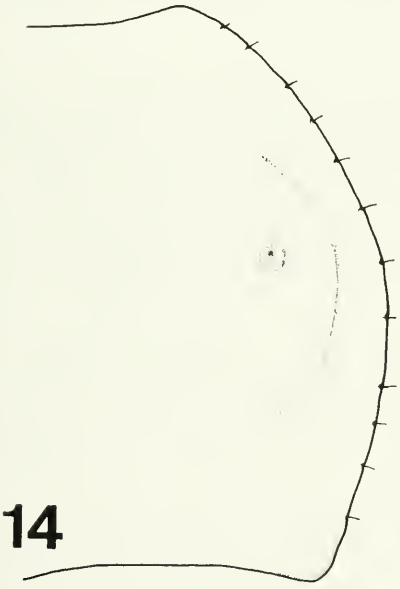
Elytron: Randomly distributed with zero to seven small dark tubercles, sometimes only vestigial. Surface with 5 parallel costae including epipleural and sutural margin. Costae 2 and 3 fused on apical knobs. Costa 4 very feebly developed and sometimes hardly visible. Intervals slightly impressed and with setiferous punctures throughout. Humeral knobs moderately swollen. Epipleuron with aligned row of entire setae, broadest at middle. Lateral and apical margin membranous.

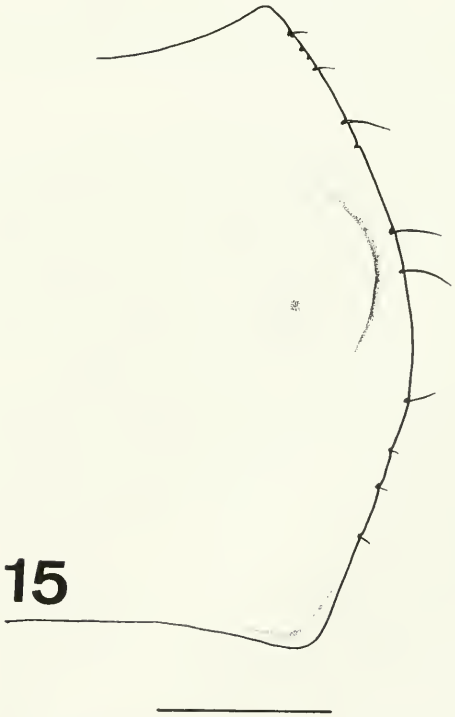
Thoracic sternites: Surface hairy with except metepisternum and metepimeron densely covered with whitish-yellow scales with slightly iridescent tinge (with illumination and magnification). Mesosternum transverse, surface of disc and mesometasternal suture depressed. Metasternum large subquadrate, weakly depressed along middle groove.

Legs: Protibia tridentate, tooth color distinctly darker than disc; basal tooth somewhat vestigial; anterior spur movable, un-

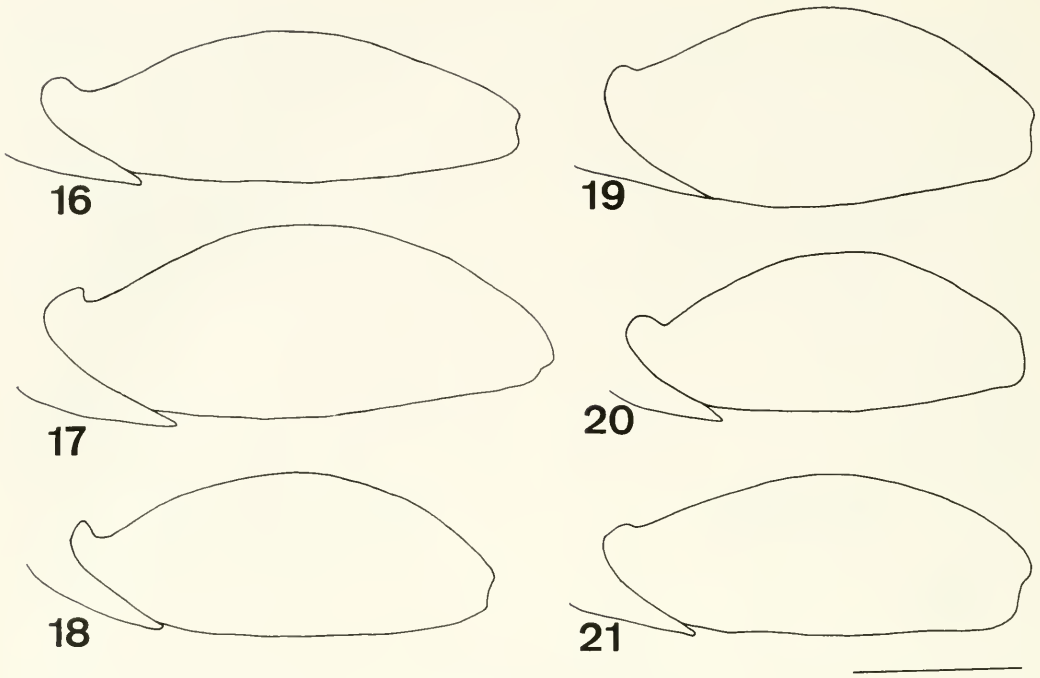








Figs. 12–15. Pronotum. 12, *Clypeolontha siamensis*. 13, *C. alboplagiata*. 14, *C. bertiae*. 15, *C. laosensis*. Scale line = 1.0 mm.

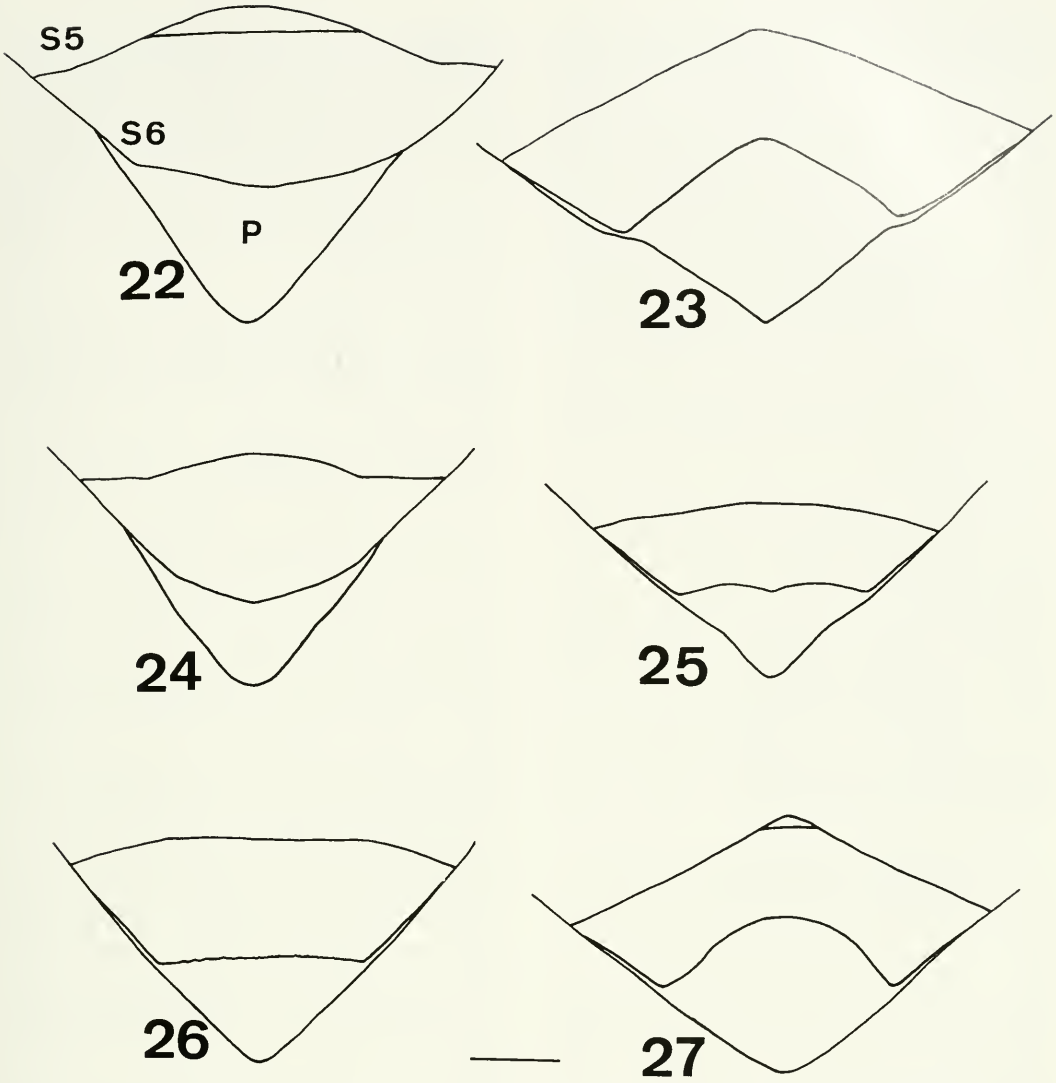


Figs. 16–21. Outlined hind femur. 16, *Clypeolontha siamensis*, male. 17, *C. siamensis*, female. 18, *C. alboplagiata*, male. 19, *C. alboplagiata*, female. 20, *C. bertiae*, female. 21, *C. laosensis*, female. Scale line = 2.0 mm.

dersized, subequal to one-fourth length of first protarsomere. Claws symmetrical, abruptly curved apically with a vertical subapical tooth at middle, one-half to two-thirds length of apical tooth. Protarsomere 1 shorter than combined length of protarsomeres 2–3; PTR = 3.0:1.7:1.6:1.6:2.7. Pro- and mesofemora transversely flattened, surface densely clothed with long, yellowish white pile. Hind femur stout (Fig. 16) with shorter pile than that on pro- and mesofemora, about 2.5 times as wide as tibia, broadest at middle; MFL/W = 2.93–3.21. Tibiae and tarsi moderately clothed with pale white setae. Meso- and metatibia with two elongate, apical spurs, outer spur of metatibiae sharper and slightly longer than length of metatarsomere 1, inner spur curved apically. Meso- and metatarsi light yellowish brown with tarsomeres 1–5 subequal in length.

Abdomen: Sternites moderately punctate; segments 1–6 continuous with wide maculation along lateral edges consisting of white scales with weakly iridescent tinge. Intervening surface shallowly setiferously punctate, with less stout and more sparsely distributed setae than those on dorsum; transversely sparsely intermixed with longer setae. Sternites 2–5 weakly fused medially, not well defined. Sternite 5 with posterior margin moderately arc-shaped centrally sometimes exposing intersegmental membrane (Fig. 22). Pygidium triangular; apex distinctly prolonged, longitudinally convex, somewhat abruptly declivious on apical one-fourth when viewed laterally (Fig. 28); width approximately equal to length; PgW/H = 1.08–1.22; marginate laterally and becoming smooth apically. Dorsal and ventral surface densely covered with tiny setae same as on dorsum, sparsely intermixed with longer setae which becoming denser on apical margin.

Male genitalia: Parameres strongly asymmetrical with apices irregularly broad-



Figs. 22–27. Outlined abdominal sternites 5–6 in ventral view. 22, *Clypeolontha siamensis*, male. 23, *C. siamensis*, female. 24, *C. alboplagiata*, male. 25, *C. alboplagiata*, female. 26, *C. bertiae*, female. 27, *C. laosensis*, female. S = sternite; P = pygidium.

ened, contracted dorsomedially, and fused at base (Fig. 34); right paramere with a inward spine on basal fourth and not fused when viewed ventrally (Fig. 35). In lateral aspect parameres asymmetrically concave and sharpened forwardly (Figs. 36, 38). Basal piece and paramere approximately equal in length.

Female.—BL = 19.7–20.7 mm.; BW = 9.3–10.0 mm; BL/BW = 2.04–2.17. Similar to male except with stouter and more robust shape (Fig. 4); BW/HW = 1.76–1.94, mean = 1.84; antennal club 6-segmented, compact and club length longer than basal segments 2–4, the first club segment one-half to one-third length of rest, three basal segments each one-half as wide as first one; apical segment of maxillary palpus subequal to combined length of segments 2–3; mean MPR = 1.9:1.4:3.5 (Fig.

42); protibia broader and more robust, anterior tooth broadened; mean PTR: 3.0:1.2:1.1:1.2:2.5; hind femur stouter and more rounded (Fig. 17); MFL/W = 2.34–2.56; the longer metatibial spur more or less stouter; abdomen dorsoventrally inflated; posterior edges of abdominal sternites 5 and 6 anteriorly with point-curved medially (Fig. 23); pygidium broadened basally with apex roundly inflated, slightly elongate and concave in lateral view (Fig. 29); PgW/H = 1.17–1.25.

Distribution.—Montane areas of northern Thailand near the border of Burma (Myanmar) (Fig. 46).

Remarks.—Itoh (1995) misidentified several specimens of this species as *C. alboplagiata* which were collected from the neighboring areas of the type locality, although he noted differences of the relative length of the first antennal club segment and the remainder in the female.

Etymology.—The specific epithet is named for Siam, the former name of collecting place of this species.

Clypeolontha alboplagiata (Brenske), **new combination**
(Figs. 3, 5, 9, 11, 13, 18, 19, 24, 25, 30, 31, 37, 39, 40, 41, 43)

Melolontha alboplagiata Brenske 1898: 236 (*nec* Itoh, 1995: 202); Dalla Torre 1912: 267 (catalog); Sabatinelli 1993: 615 (catalog).

Male diagnosis.—Male: Antennal club about 2.2 times length of stem; mean ASR = 1.3:0.5:1.8; labrum shape triangular; pronotal midline not observed, angles obtuse; protarsomere 1 longer than combined length of protarsomeres 2 and 3 (PTR = 3.0:1.2:1.1:1.2:2.5); hind femur broadly stout (MFL/W = 2.42–2.50); abdominal sternite 5 with posterior edge slightly arc-shaped centrally; apex of pygidium moderately prolonged; PgW/H = 1.00–1.03; paramere strongly curved laterally at basal one-fourth, oblique ridge along right paramere, apex turned inwardly and thinned apically.

Description.—Male. *Body:* Oblong (Fig. 3), sides subparallel medially Dorsal surface densely covered with short yellowish-brown to whitish-yellow setae, all similar in length. BL = 16.8–17.0 mm; BW = 7.8–8.0 mm; BL/BW = 2.13–2.15. Basal color reddish brown.

Head: Surface densely to confluently punctate, punctures moderately large, each bearing a short seta. Antenna 10-segmented with 7-segmented clubs; lamellae slightly outwardly curved, about 2.2 times length of stem; first basal segment wider than third one; mean ASR = 1.3:0.5:1.8. Clypeus transverse, shallowly depressed anteriorly, weakly emarginated; sides gradually rounding to biarcuate apex; middle of anterior margin inwardly depressed at tip (Fig. 9); clypeo-frontal suture moderately developed; frons slightly narrowed making eyes large. Labrum moderately grooved with respect to clypeus; transversally symmetrical, strongly bilobed and each triangular, one-third width of clypeal base, depressed laterally (Fig. 11), visible dorsally, moderately protuberant. Maxillary palpus light yellowish brown, 4-segmented; apical palpomere spindly elongate, truncate, subequal in length to palpomeres 2–3, each with a dorsal concavity. Labial palpus 3-segmented; apical palpomere subcylindrical and glabrous.

Pronotum: Moderately transverse, widest at middle, slightly narrowing posteriorly, weakly convex. Surface densely punctate, punctures evenly distributed, each with a tiny seta; anterior margin weakly emarginate. Midline not visible. Discal sides of pronotum irregularly convex at middle, each with a vestigial concavity (Fig. 13). Laterally, marginal serration poorly developed with feeble emargination, anterior and posterior angles obtuse, less protuberant (Fig. 13). Scutellum wider than long, apically rounded, moderate in size.

Elytron: Surface with 5 parallel costae including along epipleural margin and su-

tural margin. Costae 2 and 3 fused on apical knobs of elytron. Costae 4 very feebly developed and sometimes hardly visible. Intervals slightly impressed and with setiferous punctures throughout. Humeral knobs moderately swollen. Epipleuron with aligned row of entire setae, broadest at middle. Lateral and apical margins membranous.

Thoracic sternites: Surface hairy except metepisternum and metepimeron densely covered with whitish-yellow, slightly iridescent scales (with illumination and magnification). Mesosternum transverse, surface of disc and mesometasternal suture depressed. Metasternum large, subquadrate, weakly depressed along middle groove.

Legs: Protibia tridentate, tooth color distinctly darker than disc; basal tooth somewhat vestigial; anterior spur movable, undersized, subequal to one-fourth length of first protarsomere. Claws symmetrical, abruptly curved apically with a vertical subapical tooth at middle, one-half to two-thirds length of apical tooth. Protarsomere 1 longer than combined length of protarsomeres 2 and 3; mean PTR = 3.0:1.2:1.1:1.2:2.5. Femora of front and middle legs transversely flattened, surface densely clothed with long, yellowish-white pile. Hind femur more stout broadly (Fig. 18) with shorter pile than that on pro- and mesofemora; about 2.5 times as wide as tibia, broadest at middle; MFL/W = 2.42–2.50. Tibiae and tarsi moderately clothed with pale white setae. Meso- and metatibiae with two elongate, apical spurs, outer spur of metatibia sharper and slightly longer than length of metatarsomere 1, inner spur curved apically. Meso- and metatarsi light yellowish brown with tarsomeres 1–5 subequal in length.

Abdomen: Sternites moderately punctate; segments 1–6 continuous with wide maculation along lateral edges consisting of white scales with weakly iridescent tinge. Intervening surface shallowly setiferously punctate, with less stout and more sparsely distributed setae than those on dorsum; transversely sparsely intermixed with longer setae. Sternites 2–5 weakly fused medially, not well defined. Sternite 5 with posterior edge deeply, angularly emarginate (Fig. 24). Pygidium triangular; apex moderately prolonged and somewhat weakly depressed on apical one-third when viewed laterally (Fig. 30); width subequal to length; PgW/H = 1.00–1.03; marginate laterally and becoming smooth apically. Surface densely covered with tiny setae as on dorsum, sparsely intermixed with longer setae and becoming denser on apical margin.

Male genitalia: Paramere moderately asymmetrical, strongly curved laterally at basal one-fourth and fused at base; oblique ridge along right paramere to fused base (Fig. 40). Apex turned inwardly and thinned apically when viewed ventrally (Fig. 41). In lateral aspect, paramere at basal one-third concave and sharpened anteriorly (Figs. 37, 39). Basal piece and paramere approximately equal in length.

Redescription of female.—Body and legs dark brown to reddish brown; clothed with pale white setae (Fig. 5). BL = 19.8–20.1 mm.; BW = 8.8–9.0 mm; BL/BW = 2.23–2.25. Sexual dimorphism in stouter shape with dorsoventrally convex; BW/HW = 1.62–1.66, mean = 1.64; surface clothed with stouter pale white setae; antennal club 6-segmented, compact length subequal to basal segments 2–4, first club segment one-fourth length of rest, third basal segments each half as wide as first; apical segment of maxillary palpus longer than the combined length of segments 2–3; mean MPR = 1.6:1.3:3.7 (Fig. 43); protibia broader and more robust; anterior tooth longer than in male and broadened; mean PTR = 3.0:1.1:1.1:1.2:2.8; anterior and posterior angle of pronotum obtuse, less protuberant; hind femur stouter and roundly inflated (Fig. 19), MFL/W = 2.08–2.18; longer metatibial spur somewhat stouter than in male; abdomen dorsoventrally inflated; posterior edge of abdominal sternite 5 smooth, sternite 6 shallowly biarcuate (Fig. 25); pygidium broadened basally with apex somewhat

sharpened; slightly elongate and concave in lateral view (Fig. 31); PgW/H = 1.11–1.14.

Material examined.—Holotype ♀ at ZMHB labeled separately as follows: "Type(P)//India, Sikkim, ex coll. Fruhstorfer(P)//coll. Brenske(P)//Melolontha alboplagiata, type, Brsk, (H)//Zool. Mus Berlin(P). 2 ♂ and 1 ♀ are placed in ISNB labeled as: Sikkim, Kurseong, R. P. Bretaudeau, 1894(P)//ex Museo Oberthur(P)(1 ♂). British Bootang, L. Durel, 1899(P)//ex Museo Oberthur(P)(1 ♂ and 1 ♀). 2 ♂ and 1 ♀ in BMNH labeled as: Himalaya(H)// Bowring. 63 47*(P)//Melolontha(S. G. Schonherria Burm. n. sp.)(H)(1 ♂). Allahauad(W)?//Bowring. 63 47*(P)//. Determined from description. G. J. A.(P) Melolontha alboplagiata Brsk(W)(1 ♀). Atkinson Coll. 92-3.(P)(1 ♂).

Distribution.—Eastern Himalayan areas, including Sikkim and Bhutan (new record) (Fig. 46).

Remarks.—In his original description, Brenske (1898) placed that *C. alboplagiata* with the typical *Melolontha* species and distinguished them from *M. albidiventris* Fairmaire, *M. cochinchinae* Brenske, *M. rubiginosa* Fairmaire, and *M. costata* Nonfried by differences of the clypeus, pygidium, and first antennal club segment of the females and therefore considered them as an unique group. We agree that *C. alboplagiata* should be recognized as an distinct group but we reject the concept of so-called typical *Melolontha* applied at that time because it does not satisfy today's systematic requirement and may cause more taxonomic uncertainty. However, after careful comparison of the types and other material, the systematic position of the above-mentioned species by Brenske (1898) within *Melolontha* suggest further revisionary work.

Clypeolontha bertiae Li and Yang, new species

(Figs. 7, 14, 20, 26, 32, 44)

Type series.—Holotype ♀ (deposited in NMNH) with label data in handwritting as follows: Pukhieo, Chiaya poon, NE Thailand, 5-V-1986, P. EK-Amnuay. 4 ♀ paratypes: one with the same data as holotype deposited in MNHN; one in ISNB, with label data as follows: Laos, Luang Prabang: Ban Na Gnan. 20. V. 1920. R. V. de Salvaza(P). Specimen (in ISNB) condition: right protarsus, middle and hind legs missing; anterior two segments of left protarsus missing. The remaining two paratypes is in BMNH with identical printed label data as follows: At light//N.E. Thailand: 800m., Phu Khieo Wildlife Sanctuary, 16°30′N, 101°46′E//Chaiyaphum Province, Khon San. 13–15. V.1988//Evergreen rain forest. M. J. D. Brendell. B. M. 1988-183.

Description.—Female. *Body:* Oblong (Fig. 7), dorsoventrally convex and sides subparallel medially. BL = 17.9–18.5 mm; BW = 7.8–7.9 mm; BL/BW = 2.28–2.35. *Head:* Deeply rufous brown to lightly reddish brown. Surface distinctly punctate, punctures large, each bearing a tiny, pale white to yellowish-brown seta, brighter on sides of eyes. Antenna 10-segmented with 6-segmented club; first club segment half to two-thirds length of rest; first basal segment subequal in length to third. Clypeus transverse, very shallowly depressed anterior to marginated edge; sides gradually rounding to biarcuate apex; middle of anterior margin inwardly depressed at tip; clypeo-frontal suture moderately developed. Labrum moderately grooved with respect to clypeus; transversally symmetrical, strongly bilobed, moderately declivous laterally, one-third width of clypeal base, visible dorsally, moderately protuberant. Maxillary palpus yellowish-brown; 4-segmented; apical palpomere spindly elongate, truncate, equal to combined length of segments 2–3 (Fig. 44); mean MPR = 2.0:1.5:3.5. Labial palpus 3-segmented; apical palpomere subcylindrical and glabrous.

Pronotum: Rufous brown. Moderately transverse, widest at middle, slightly narrowing posteriorly, disc moderately convex. Surface densely finely punctate, punctures evenly distributed, each with a pale white to yellow seta; anterior margin weakly

emarginate. Midline not visible. Discal sides of pronotum irregularly convex at middle, each with a shallow concavity (Fig. 14). Laterally, marginal serration poorly developed with feeble emargination; anterior and posterior angle weakly protuberant (Fig. 14). Scutellum wider than long, apically rounded, moderate in size.

Elytron: Brightly rufous yellow to rufous brown. Mean BW/HW = 1.73. Surface clothed with pale white to yellow setae; bearing 5 parallel costae on each elytron including along epipleural margin and sutural margins. Costae 2 and 3 fused on the apical knobs of elytron. Costae 4 very feebly developed and hardly visible. Intervals slightly impressed and with setiferous punctures throughout. Humeral knobs moderately swollen. Epipleuron with aligned row of smaller entire setae, broadest at middle. Lateral and apical margin membranous.

Thoracic sternites: Surface hairy except metepisternum and metepimeron densely covered with whitish-yellow scales with slight iridescent tinge (with illumination and magnification). Mesosternum transverse, surface of disc and mesometasternal suture depressed. Metasternum large, subquadrate, weakly depressed along middle groove.

Legs: Protibia tridentate, tooth color darker than disc; basal tooth somewhat obsolete; anterior spur movable, undersized, subequal to one-fourth the length of first protarsomere. Claws symmetrical, abruptly curved apically with a vertical subapical tooth at middle, two-thirds length of apical tooth. Pretarsus reddish brown; broadened laterally; protarsomere 1 longer than combined length of protarsomeres 2 and 3; PTR = 3.3:1.4:1.2:1.4:2.2 (n = 4). Pro- and mesofemora transversely flattened, surface densely clothed with long, yellowish-white pile. Meso- and metatibiae and tarsi lightly yellowish brown; metatarsal spurs reddish brown. Hind femur roundly inflated (Fig. 20) with shorter pile than those on pro- and mesofemora; MFL/W = 2.34–2.45.

Abdomen: Dorsoventrally inflated. Sternites transversely rugose, moderately punctate; segments 1–6 continuous with wide maculation along lateral edges consisting of white scales with weakly iridescent tinge. Intervening surface shallowly setiferously punctate with setae same as on dorsum, transversely intermixed with very sparse longer setae. Sternites 2–5 weakly fused medially, not well defined. Posterior edges of sternites 5 and 6 smooth, sternite 6 with feeble irregular serration (Fig. 26). Pygidium deeply reddish to lightly rufous brown; densely clothed with pale white to yellow setae sparsely intermixed with longer setae; triangular; in lateral view apex moderately elongate, smoothly declivous apically with apex sharpened (Fig. 32); marginate laterally then decreased apically. PgW/H = 1.08–1.12. Apex dorsoventrally with a terminal tuft of denser setae.

Distribution.—Some 200 km north of Vientiane, Laos, and the low montane area of northeastern Thailand (Fig. 46).

Remarks.—We describe *Clypeolontha bertiae* from only five females because those diagnostic characters found in the female types of *C. siamensis,* referring to both *C. siamensis* and *C. alboplgiata,* are useful and stable enough to separate interspecific females. Those distinguishing characters are given in the key.

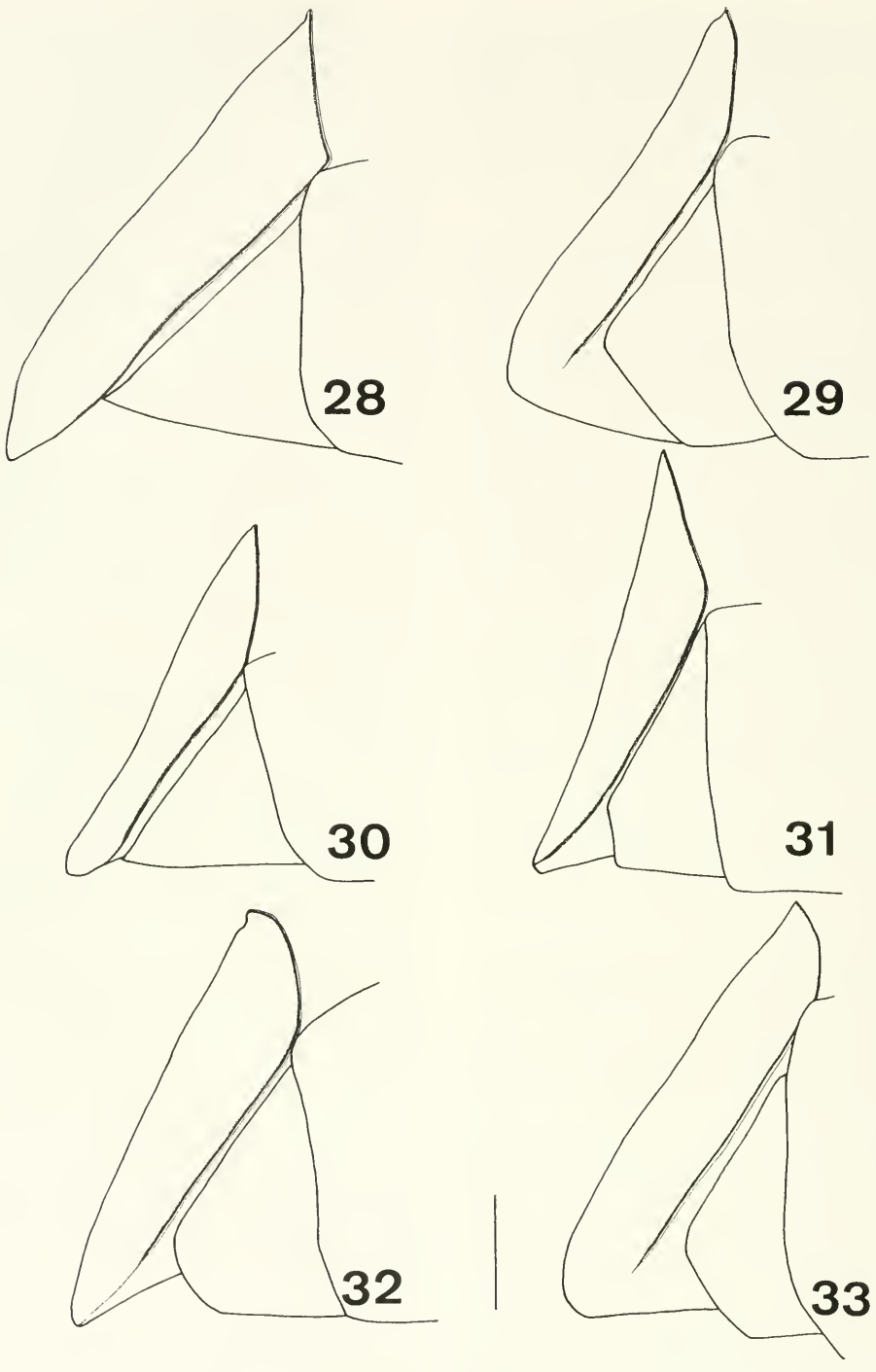
Etymology.—Named for Dr. Nicole Berti who helped the senior author at Muséum national d'Histoire naturelle, Paris, in 1997.

Clypeolontha laosensis Li and Yang, new species

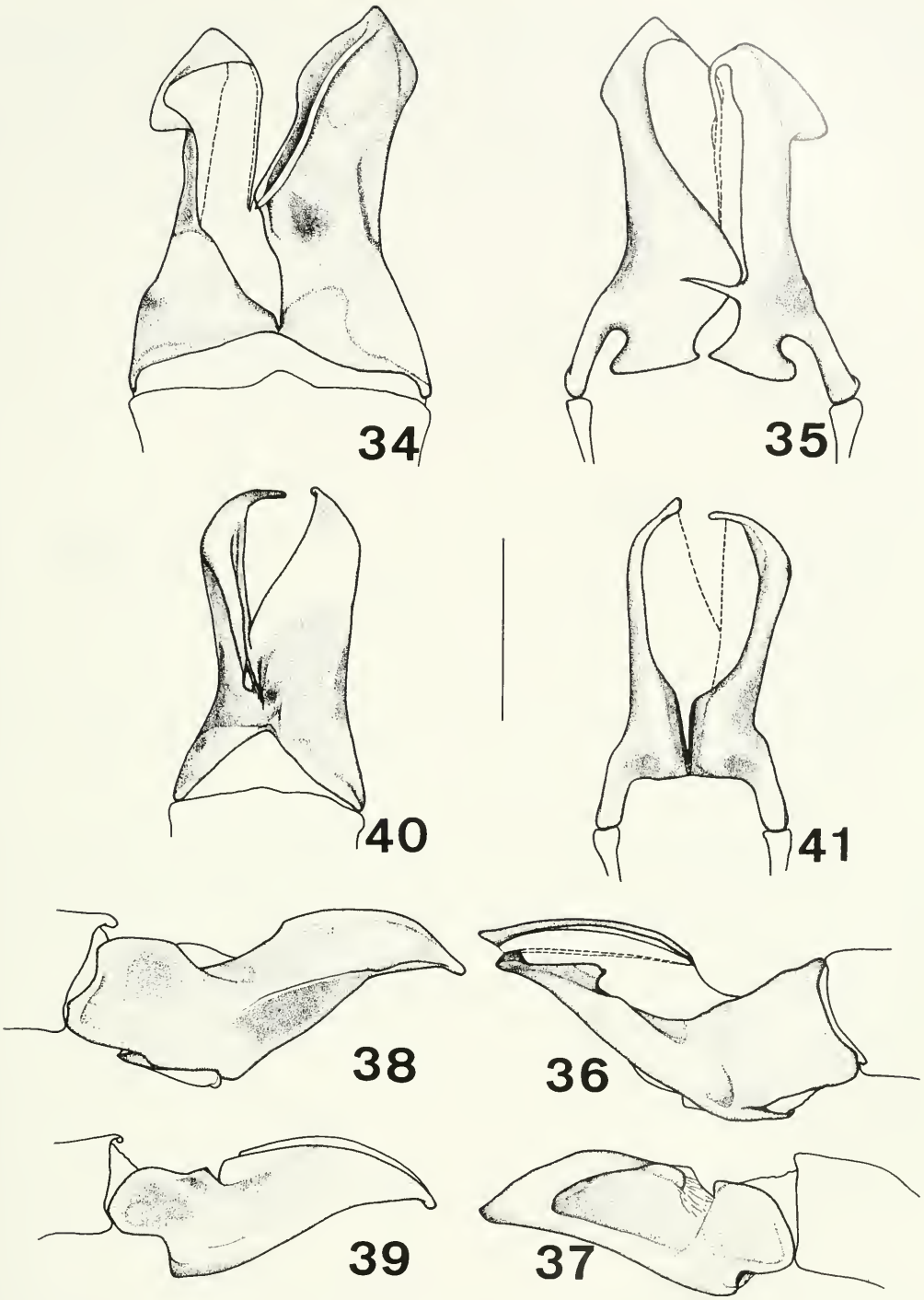
(Figs. 6, 15, 21, 27, 33, 45)

Type.—Holotype ♀ (deposited in ISNB) labeled as follows: Laos(P), Nam Tien(H), le(P), 14-IV(H), 191(P)8(H), R. Vitalis de Salvaza(P).

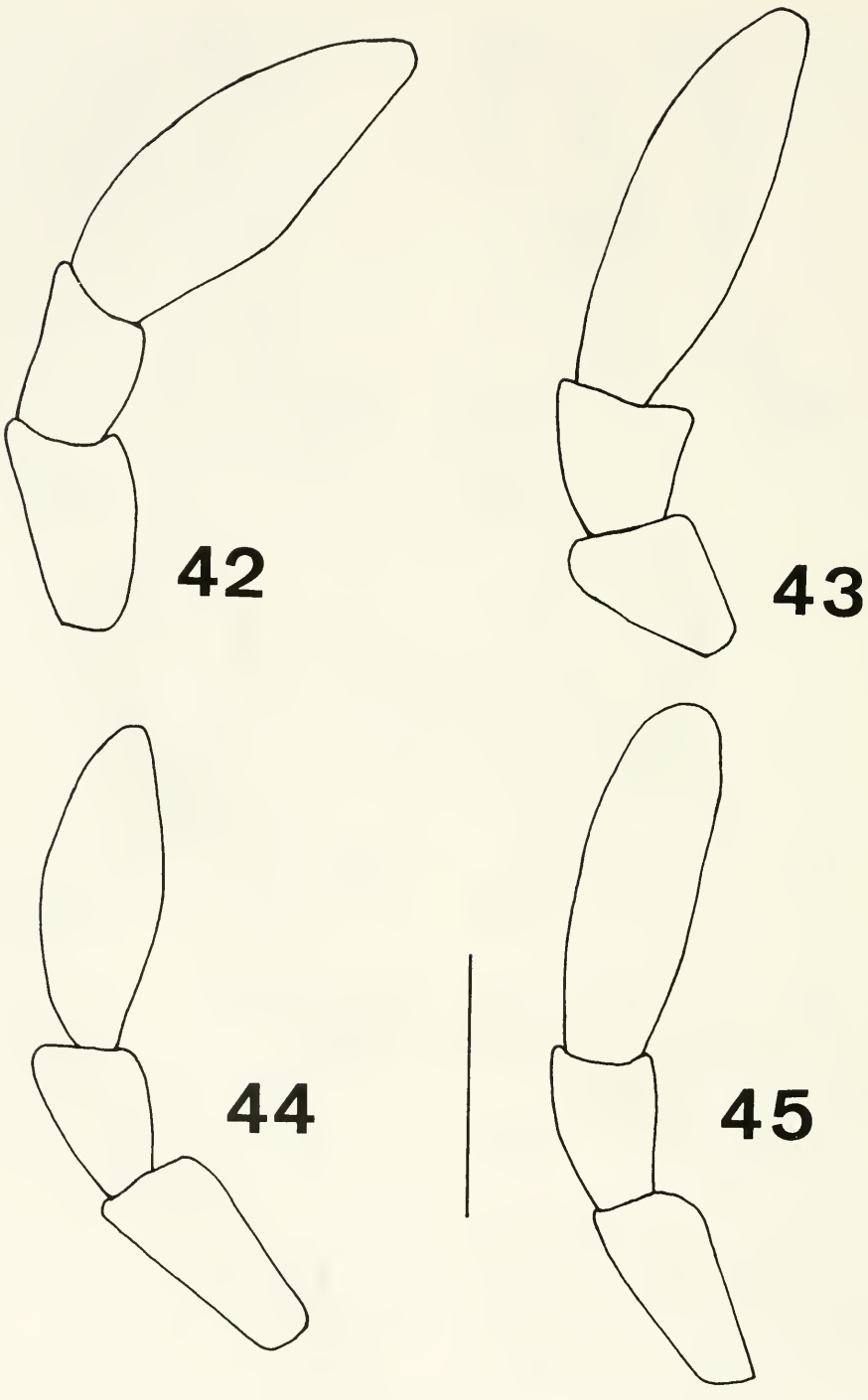
Description.—Female. *Body:* Oblong (Fig. 6), dorsoventrally convex and sides subparallel medially. BL = 17.2 mm; BW = 7.5 mm; BL/BW = 2.29. Basal color dark rufous brown. *Head:* Surface distinctly punctate, punctures large, each bearing a tiny, yellowish-brown seta, brighter on



Figs. 28–33. Pygidium, right lateral view. 28, *Clypeolontha siamensis*, male. 29, *C. siamensis*, female. 30, *C. alboplagiata*, male. 31, *C. alboplagiata*, female. 32, *C. bertiae*, female. 33, *C. laosensis*, female. Scale line = 1.0 mm.



Figs. 34–41. Male genitalia. 34, 35, 36, 37, *Clypeolontha siamensis*. 38, 39, 40, 41, *C. alboplagiata*. 34, 40, Dorsal view. 36–37, Right lateral view. 38–39, Left lateral view. 35, 41, Ventral view. Scale line = 1.0 mm.



Figs. 42–45. Female outlined maxillary palpomeres 2–4. 42, *Clypeolontha siamensis*. 43, *C. alboplagiata*. 44, *C. bertiae*. 45, *C. laosensis*. Scale line = 0.5 mm.

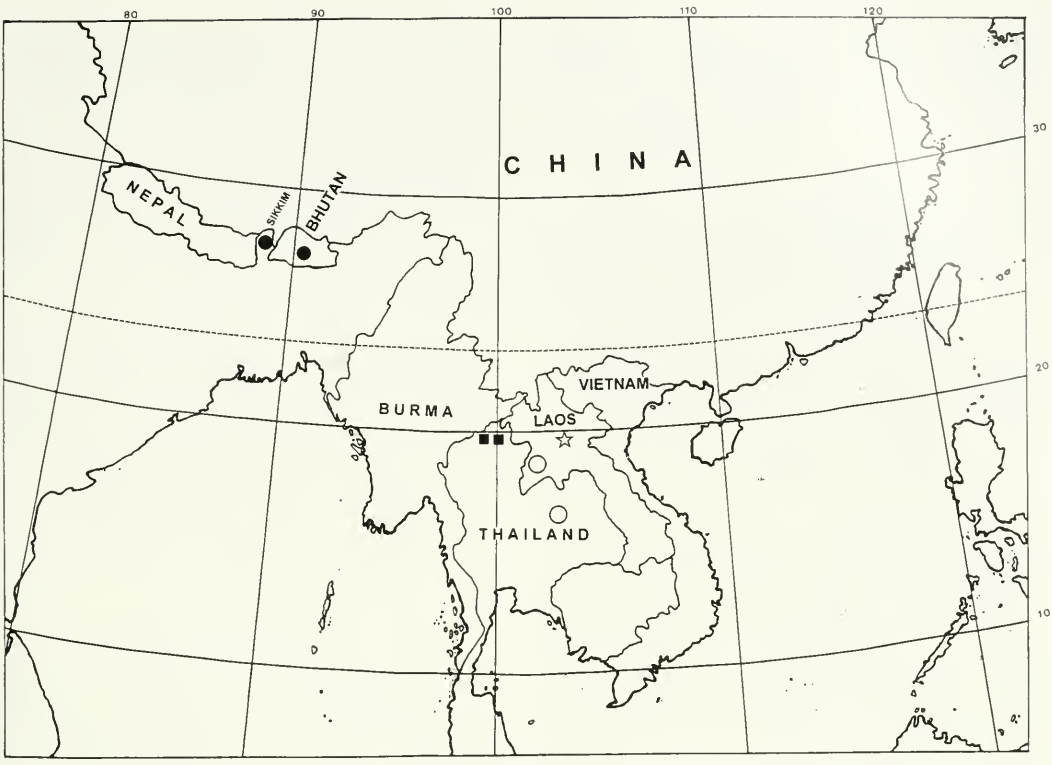


Fig. 46. Distribution. Solid square = *Clypeolontha siamensis*; solid circle = *C. alboplagiata*; open circle = *C. bertiae*; star = *C. laosensis*.

sides of eyes. Antenna 10-segmented with 6-segmented club; first club segment half length of rest; first basal segment subequal in length to third. Clypeus transverse, moderately depressed anterior to marginated edge; sides gradually rounding to biarcuate apex; middle of anterior margin inwardly depressed at tip; clypeo-frontal suture moderately developed. Labrum moderately grooved with respect to clypeus; transversally symmetrical, strongly bilobed, moderately declivous laterally, one-third width of clypeal base, visible dorsally, moderately protuberant. Maxillary palpus dark yellowish brown; 4-segmented; apical palpomere spindly stout, truncate, shorter than combined length of segments 2–3 (Fig. 45); MPR = 1.8:1.3:2.7. Labial palpus 3-segmented; apical palpomere subcylindrical and glabrous.

Pronotum: Moderately transverse, widest at middle, slightly narrowing posteriorly, weakly convex. Surface densely punctate, punctures more or less irregularly distributed, each with a pale white seta; anterior margin weakly emarginate. Midline very shallowly depressed, clothed with very tiny, brownish setae. Discal sides of pronotum irregularly convex at middle, each with a vestigial concavity (Fig. 15). Laterally, marginal serration poorly developed with feeble emargination; anterior angle acute, protuberant; posterior angle obstuse (Fig. 15). Scutellum wider than long, apically rounded, moderate in size.

Elytron: BW/HW = 1.91. Surface clothed with pale white setae, tending yellow basally; bearing 5 parallel costae on each elytron including along epipleural margin and sutural margin. Costae 2 and 3 fused on the apical knobs of elytron. Costae 4 very feebly developed and hardly visible.

Intervals slightly impressed and with setiferous punctures throughout. Humeral knobs moderately swollen. Epipleuron with aligned row of smaller, brownish entire setae, broadest at middle. Lateral and apical margins membranous.

Thoracic sternites: Surface hairy except metepisternum and metepimeron densely covered with whitish-yellow scales with slight iridescent tinge (with illumination and magnification). Mesosternum transverse, surface of disc and mesometasternal suture depressed. Metasternum large, subquadrate, weakly depressed along middle groove.

Legs: Protibia tridentate, tooth color distinctly darker than disc; basal tooth somewhat obsolete; anterior spur movable, undersized, subequal to one-third length of first protarsomere. Claws symmetrical, abruptly curved apically with a vertical subapical tooth at middle, two-thirds length of apical tooth. Pretarsus dark yellowish brown; broadened laterally; protarsomere 1 longer than combined length of protarsomeres 2 and 3; PTR = 3.0: 1.4:1.2:1.2:2.3. Femora dark rufous brown. Pro- and mesofemora transversely flattened, surface densely clothed with long, yellowish-white pile. Hind femur slightly transversely inflated (Fig. 21) with shorter pile than those on pro- and mesofemora; MFL/W = 2.61. Tibiae and tarsi moderately clothed with pale white setae. Meso- and metatibia with 2 elongate, apical spurs, outer spur of metatibiae sharper and slightly longer than length of metatarsomere 1, inner spur curved apically. Meso- and metatarsi dark yellowish brown with tarsomeres 1–5 subequal in length.

Abdomen: Dorsoventrally inflated. Sternites transversely rugose, moderately punctate; segments 1–6 continuous with wide maculation along lateral edges consisting of white scales with weakly iridescent tinge. Intervening surface shallowly setiferous punctate with whitish-yellow setae; transversely intermixed with very sparsely longer setae. Sternites 2–5 weakly fused medially, not well defined. Posterior edge of sternite 5 with distinct point-curve, sternite 6 deeply, broadly emarginate (Fig. 27). Pygidium reddish brown; wider than long; triangular; densely clothed with yellowish-brown setae sparsely intermixed with longer setae; in lateral view, apex slightly elongate, smoothly declivous apically with apex rounded (Fig. 33); marginate laterally and smooth apically. PgW/H = 1.18. Apex dorsoventrally with a terminal tuft of denser setae.

Distribution.—Northern Laos, roughly 19°34′N, 103°42′E (Fig. 46).

Remarks.—*Clypeolontha laosensis* is described from a single female. Geographically and morphologically, it is close to *C. bertiae,* but it may be separated from it by the diagnostic characters in the key.

Etymology.—The specific epithet is from the country of collection.

Acknowledgments

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DASYMUTILLA TOMBERLINI, A NEW SPECIES OF VELVET ANT (HYMENOPTERA: MUTILLIDAE) FROM NEW MEXICO

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Abstract.—***Dasymutilla tomberlini*** is a new species of velvet ant (Hymenoptera: Mutillidae) collected in extreme southwestern New Mexico. It is distinguished by the presence of only yellow pubescence, by the complete absence of black pubescence, and by the smooth anterior surface of the first gastral tergite. Eleven specimens were examined, all collected in pitfall traps.

Key Words: *Dasymutilla tomberlini,* new species, Mutillidae, Hymenoptera

In March of 1996, specimens of velvet ants (Hymenoptera: Mutillidae) from the Carnegie Museum of Natural History collection were sent to me for identification by C. W. Young. Among those specimens was a series of 11 females of *Dasymutilla* Ashmead from extreme southwestern New Mexico that was determined to be a new species. A diagnosis and description follow.

Dasymutilla tomberlini Manley, new species

Diagnosis.—This species has the integument reddish throughout and is densely clothed over most of the body with yellowish pubescence. All pubescence is of this color. A scutellar scale is present and the antennal scrobes are carinate. There is no genal carina and the genae are relatively smooth and shining. The anterior face of the first abdominal tergite is smooth and shining, devoid of punctation or pubescence. The pygidium is finely rugose, almost granulate.

Description.—Female: Length, 10.6–15.0 mm. Head reddish, densely clothed with yellowish recumbent pubescence; some long, erect yellow pubescence on vertex; mandible acute at tip, with an inconspicuous inner tooth about one-third distance from tip; clypeus evenly convex on anterior margin, but concealed by yellowish pubescence; scape weakly carinate, smooth and shining, clothed with yellowish pubescence; first flagellomere long, about length of second and third united, remaining flagellomeres subequal in length; antennal scrobes distinctly carinate; front and vertex coarsely punctate, but with dense yellow pubescence concealing sculpture; gena smooth and shining, with shallow, well-separated punctures, lacking a genal carina, and concealed with yellow pubescence; head width 2.1–2.6 mm; relative width of head to thorax 0.75.

Thorax reddish, densely clothed with erect and recumbent yellow pubescence; dorsum of thorax longer than broad (3.2–4.3 mm long × 2.7–3.5 mm wide); scutellar scale present and conspicuous, as well as a transverse, sinuate carina immediately anterior to scutellar scale; cephalic margin of pronotum evenly rounded, not emarginate medially; entire thorax densely covered

with yellow pubescence, obscuring punctation.

Abdomen reddish, densely clothed with erect and recumbent yellow pubescence, except anterior face of first gastral tergite smooth and shining, devoid of pubescence except for apical fringe; pygidium devoid of pubescence, and disk of second sternite with only a few scattered hairs; disk of second tergite smooth and shining, with sparse, shallow punctures; remainder of sculpture concealed by dense yellow pubescence; pygidium finely rugose, almost granulate; first sternite with a distinct carina about one-third its length, elevated distally to form a tooth.

Legs reddish, smooth, and shining, conspicuously clothed with yellow pubescence.

Most type specimens (7) longer than 13.0 mm. Thorax in each specimen longer than broad, with width:length ratio generally about 0.8:1.0. Head width distinctly narrower than thoracic width.

Male: Unknown.

Holotype.—♀, Antelope Pass, Peloncillo Mountains, Hidalgo County, New Mexico, July 1990 (Barney Tomberlin), collected by pitfall trap, deposited in the collection of the Carnegie Museum of Natural History.

Paratypes.—10 ♀, same data as holotype. Paratypes deposited in the Carnegie Museum of Natural History (7), and with the author (3).

Etymology.—Named after Barney Tomberlin who collected the series of specimens.

Discussion.—This species superficially resembles *Dasymutilla magna* (Cresson). However, under microscopic examination, it is easily distinguished from *D. magna.* The latter has the genae as coarsely punctate as the front and vertex and possesses a genal carina. In *D. tomberlini,* although obscured by the dense pubescence, the genae are relatively smooth and shining, much less coarsely punctate than the front and vertex, and a genal carina is lacking. In Mickel's (1928) key to *Dasymutilla,* this species keys to couplet 81, which includes *D. satanas* Mickel and *D. sackenii* (Cresson). In Mickel's more recent (1936) key to *Dasymutilla,* it keys to couplet 87, which includes the same two species. This species can be distinguished from all of the above-mentioned species by the total lack of black pubescence and by the smooth and shining anterior margin of the first gastral tergite.

This species is known only from the type series, collected in pitfall traps designed to collect reptiles, near the Arizona border in extreme southwestern New Mexico. In spite of extensive personal collecting and examination of numerous collections including specimens collected from the same general locale, no other specimens of this species have been encountered. Due to the collection method, only females were collected.

None of the species of *Dasymutilla* listed in Krombein (1979) for which only the male is known seem to be likely candidates as the male of this species. Although *D. candida* Mickel is somewhat similar in color and geographic range (being found in southeastern Arizona), it is much smaller (length 8–9 mm) than *D. tomberlini* (10–15 mm). It seems more likely that *D. candida* represents the unknown male of *D. thetis* (Blake) than the present species.

Acknowledgments

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA WHEELERI* CURRAN (DIPTERA: TEPHRITIDAE) ON ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea wheeleri* Curran is a multivoltine, florivorous fruit fly (Diptera: Tephritidae) infesting flower heads of a wide variety of Asteraceae in California and the western half of the United States. Four new host-plant genera and five new species records are reported. To date, *T. Wheeleri* is known from seven tribes, 15 subtribes, 28 genera, and 47 species of hosts. The egg, first through third instar larvae, and puparium are described and figured for the first time. The egg pedicel has one or two rows of aeropyles. The interspiracular processes of the first instar are large, broad, and multibranched. The anterior thoracic spiracles of the second instar each bear 7–8 papillae, more than any previously studied congeneric species. The lateral spiracular complexes of the third instar are identical to that of *T. imperfecta* (Coquillett), which is the first report of two species of *Trupanea* that share the same type and number of sensilla in their metathoracic and abdominal, lateral spiracular complexes. The life cycle of *T. wheeleri* in southern California is of the aggregative type. The eggs are inserted alongside or into the corollas of florets and ovules upon which the first instars feed in closed, preblossom flower heads. Second instars feed mainly on ovules and florets of preblossom flower heads and soft achenes of open flower heads; whereas, third instars feed on soft achenes in open and postblossom flower heads. Pupariation occurs inside the mature flower heads, from which the adults emerge about the time that the achenes are shed. Several generations are produced on a variety of hosts during the spring, summer, and fall, and overwintering is as long-lived adults. Seven species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. wheeleri* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma* n. sp.? (Eurytomidae), *Eurytoma obtusiventris* Gahan (Eurytomidae), *Eurytoma veronia* Bugbee (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Mesopolobus* sp. (Pteromalidae), *Pteromalus* sp. (Pteromalidae), *Torymus* sp. (Torymidae).

Key Words: Insecta, *Trupanea,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages and adults, flower-head feeding, host-plant range, parasitoids

This is the penultimate paper in our recent series on *Trupanea,* one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California, though of little or no economic importance (Foote and Blanc 1963, Foote et al. 1993). *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until we published detailed life histories of ten species from southern California (Cavender

and Goeden 1982; Goeden 1987, 1988; Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of their immature stages (Cavender and Goeden 1982; Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). In this paper we describe the life history and immature stages of an eleventh species, *T. wheeleri* Curran.

Materials and Methods

This study was based in large part on dissections of subsamples of flower heads of Asteraceae infested by *T. wheeleri* from samples collected since 1990 in southern California in the manner described by Goeden (1985, 1992). One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-two eggs, 15 first-, 10 second-, and 12 third-instar larvae, and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials also were paired (n = 3) in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden and Teerink (1997a, b; 1998, 1999), Goeden et al. (1998a, b), Headrick and Goeden (1991), Knio et al. (1996a), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. wheeleri* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and now maintained by RDG.

Results and Discussion

Taxonomy

Adult.—*Trupanea wheeleri* was first described by Curran (1932) from a female holotype from San Diego Co., California, as *Trypanea wheeleri*. *Trypanea* is a misspelling of *Trupanea*. Curran (1932), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern of the female and male, which, unlike those of several North American *Trupanea* spp., is not overtly sexually dimorphic (Foot et al. 1993). However, sex-related, wing-pattern variations were found by RDG in *T. whee-*

Table 1. Incidences (%) of absence/complete-/incompleteness of proximal and distal rays in cell dm in wings of 423 ♂ and 376 ♀ *T. wheeleri* reared from flower heads of native Asteraceae in southern California during 1989–1997.

Left wing						Right wing					
Proximal ray			Distal ray			Proximal ray			Distal ray		
M[a]	B[a]	C[a]	M	B	C	M	B	C	M	B	C
Males											
205	186	32	0	191	232	201	183	39	1	189	233
(48.5)	(44.0)	(7.5)	(0.0)	(45.2)	(54.8)	(47.5)	(43.3)	(9.2)	(0.2)	(44.7)	(55.1)
Females											
117	197	62	0	87	289	114	200	62	0	90	286
(31.1)	(52.4)	(16.5)	(0.0)	(23.1)	(76.9)	(30.3)	(53.2)	(16.5)	(0.0)	(23.9)	(76.1)

[a] M = missing, B = broken, C = complete.

leri. Foote et al. (1993, p. 446) cautioned that the "... identification of this species must be approached with care, as the proximal ray in cell dm varies from completely present to completely absent." RDG quantified the variation in this key character in reared specimens of *T. wheeleri* from California in his research collection (Table 1). The data in Table 1 show that the proximal ray is much more prone to be missing than complete than is the distal ray in both wings of males as well as females. In nearly half of both wings examined in males, the proximal and distal rays were broken, a condition which Foote et al. (1993, p. 446) described for the proximal ray as, "... the two ends of this ray are visible as outcroppings in the dark area around vein r-m and anteriorly-directed extensions of the distal end of the elongate marking on vein CuA_1." Among females, however, the proximal ray was twice as likely to be broken than the distal ray (Table 1), and unlike the proximal ray, this broken ray in both sexes usually appeared as a posteriorly-directed outcropping arising midway between crossveins r-m and dm-cu along vein M.

Foote et al. (1993) also noted that the holotype has the proximal ray complete in one wing, but almost completely missing in the other. Indeed, in 99 (23.4%) of the 423 males and 69 (18.4%) of the 376 females examined (Table 1), the proximal and distal rays of one wing differed as to whether they were missing, broken, and complete in the other wing of the same individuals. Finally, 32 (7.6%) of all males and 17 (4.5%) of all females lacked the elongated darkening along vein CuA_1 or had this infuscation reduced, sometimes to a spot, as in some *T. actinobola* (Loew), *T. jonesi* Curran, *T. texana* Malloch, and *T. vicina* (Wulp) (Foote et al. 1993), yet all of these variants were reared along with *T. wheeleri* from the same samples of flower heads of known hosts of *T. wheeleri.* Misidentifications of such variants may explain the limited records in Foote et al. (1993) for *T. texana* from southern California, where we have not yet reared this species. This variation may also help to explain difficulties experienced in distinguishing some females of *T. actinobola* from *T. wheeleri* (Goeden et al. 1998b). In most instances, however, the infuscation along vein CuA_1 combined with the dark ray connecting the pterostigma with vein r-m that is narrower than the length of the pterostigma serve to distinguish *T. wheeleri* from all North American congeners (Foote et al. 1993).

Immature stages.—The eggs, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Twenty-seven eggs of *T. wheeleri* dissected from field-collected flower heads were white, opaque, smooth, elongate-ellip-

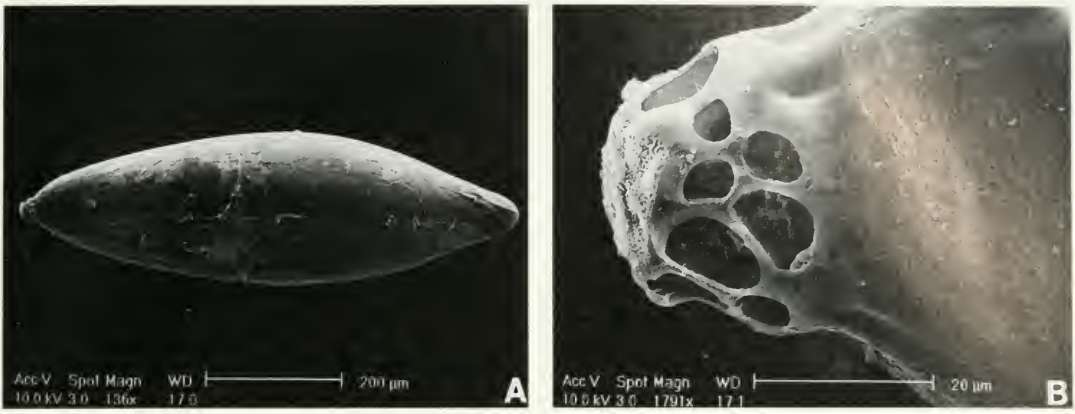

Fig. 1. Egg of *Trupanea wheeleri:* (A) habitus, anterior end to left: (B) pedicel, aeropyles.

soidal, 0.63 ± 0.003 (range, 0.58–0.64) mm long, 0.18 ± 0.003 (range, 0.16–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A); peg-like pedicel 0.02 mm long, with 1–2 rows of aeropyles (Fig. 1B).

The egg of *T. wheeleri* is similar to that of *T. bisetosa* in possessing one or two rows of aeropyles, all other species of *Trupanea* previously studied have only one row (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). The egg of *T. bisetosa* is much longer, however, than that of *T. wheeleri* (Knio et al. 1996a). The *T. wheeleri* egg also is slightly larger than the egg of *T. pseudovicina* (Goeden and Teerink 1998a), wider than that of *T. arizonensis* (Goeden and Teerink 1998b), but smaller than that of *T. imperfecta* (Teerink and Goeden 1998).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines; gnathocephalon smooth, lacking rugose pads (Fig. 2B); dorsal sensory organ a dome-shaped papilla (Fig. 2B-1, 2C-1); anterior sensory lobe (Fig. 2B-2), bears terminal sensory organ (Fig. 2C-2), pit sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4) and supralateral sensory organ (Fig. 2C-5); stomal sense organ reduced and ventrad of anterior sensory lobe (Fig. 2B-3); mouth hook bidentate (Fig. 2B-4, 2D-1); median oral lobe laterally flattened (Fig. 2B-5, D-2); labial lobe with two pore sensilla (Fig. 2D-3); a pair of integumental petals dorsad of mouth hooks (Fig. 2B-6, 2D-4); pit sensillum laterad of mouth lumen (Fig. 2D-5); minute acanthae ventrad of mouth lumen; anterior thoracic spiracle absent; caudal segment with two stelex sensilla dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears two ovoid rimae, ca. 0.008 mm in length (Fig. 2E-1), and four interspiracular processes, each with 1–2, multi-dentate branches, longest measuring 0.007 mm (Fig. 2E-2); intermediate sensory complex with a stelex sensillum (Fig. 2F-1) and a medusoid sensillum (Fig. 2F-2).

The first instar is similar in general habitus and sensory structures to previously studied *Trupanea* species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999). However, the interspiracular processes are large, broad, and apically multi-branched, and thus are far more elaborate than those of, for example, *T. arizonensis* (Goeden and Teerink 1998) and *T. conjuncta* (Teerink and Goeden 1998).

Second instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly (Fig. 3A), minute acanthae circumscribe in-

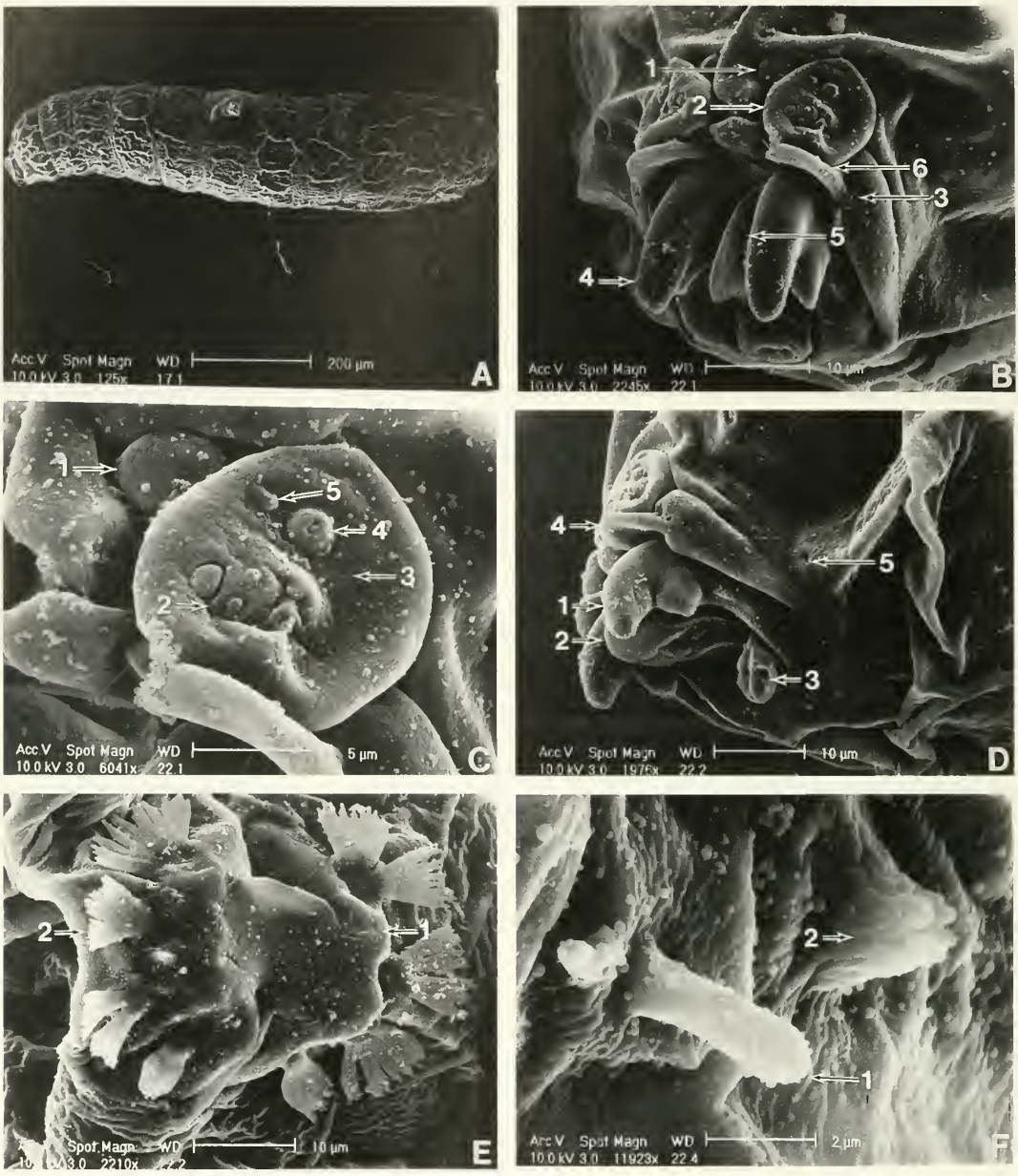

Fig. 2. First instar of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hook, 5—median oral lobe, 6—integumental petal; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon, ventral view, 1—mouth hook, 2—median oral lobe, 3—labial lobe pore sensilla, 4—integumental petal, 5—pit sensillum; (E) posterior spiracular plates, 1—rima, 2—interspiracular process; (F) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum.

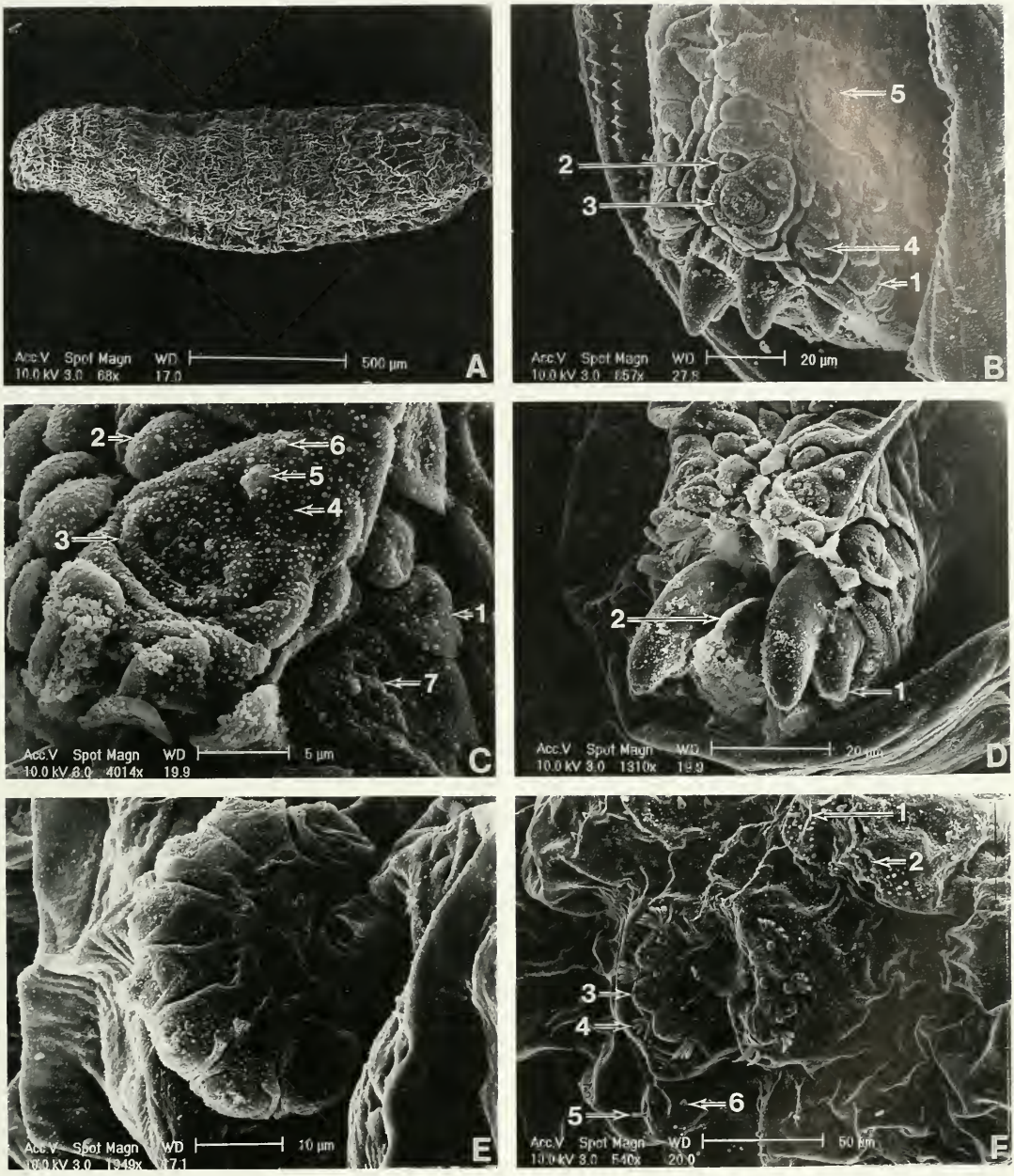

Fig. 3. Second instar of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1—serrated rugose pad, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—stomal sense organ, 5—pit sensillum; (C) anterior sensory lobe, 1—serrated rugose pads, 2—dorsal sensory organ, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—stomal sense organ; (D) gnathocephalon, anterior view, 1—mouth hook, 2—median oral lobe; (E) anterior thoracic spiracle; (F) caudal segment, 1—stelex sensillum, 2—verruciform sensillum, 3—rima, 4—interspiracular process, 5—intermediate sensory complex, stelex sensillum, 6—intermediate sensory complex, medusoid sensillum.

tersegmental lines; gnathocephalon conical (Fig. 3B); rugose pads laterad of anterior sensory lobe serrated on ventral margin (Fig. 3B-1, C-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-2); anterior sensory lobe (Fig. 3B-3), bears terminal sensory organ (Fig. 3C-3), pit sensory organ (Fig. 3C-4), lateral sensory organ (Fig. 3C-5), and supralateral sensory organ (Fig. 3C-6); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-4, 3C-7); mouth hook bidentate (Fig. 3D-1); median oral lobe laterally flattened (Fig. 3D-2); pit sensilla circumscribe gnathocephalon (Fig. 3B-5); minute acanthae circumscribe anterior margin of prothorax; rugose pads and two rows of verruciform sensilla circumscribe prothorax; anterior thoracic spiracle bears 7–8 ovoid papillae (Fig. 3E); verruciform sensilla circumscribe mesothorax; lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorsad and ventrad of posterior spiracular plate (Fig. 3F-1); two verruciform sensilla dorsolaterad of posterior spiracular plate (Fig. 3F-2); posterior spiracular plate bears three ovoid rimae, ca. 0.018 mm in length (Fig. 3F-3), and four interspiracular processes, each with 3–6 branches, longest measuring 0.01 mm (Fig. 3F-4); intermediate sensory complex with a medusoid sensillum (Fig. 3F-5) and a stelex sensillum (Fig. 3F-6).

The second instar bears serrated rugose pads laterad of the mouth lumen similar to the second instars of *T. nigricornis* and *T. pseudovicina* (Knio et al. 1996a, Goeden and Teerink 1998). The second instars of *T. imperfecta* and *T. jonesi* lack serrated rugose pads, although the third instars of both species bear serrated rugose pads (Goeden et al. 1998a, Teerink and Goeden 1998b). In the second instar of *T. wheeleri*, the anterior spiracle bears 7–8 papillae, more than any previously studied congeneric species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). The interspiracular processes are not as elaborately branched as those of the first instar.

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 4A); gnathocephalon conical (Fig. 4B), rugose pads laterad of mouth lumen serrated on ventral margin; dorsal sensory organ a dome-shaped papilla (Fig. 4C-1); anterior sensory lobe bears terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4), and supralateral sensory organ (Fig. 4C-5); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 4C-6); mouth hooks hidden in all prepared specimens; prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-1); rugose pads circumscribe prothorax posteriorad to minute acanthae (Fig. 4B-2); two rows of verruciform sensilla circumscribe prothorax posteriorad to rugose pads (Fig. 4B-3); stelex sensillum located dorsomedially (Fig. 4B-4); anterior spiracle on posterior margin of prothorax bears 3–5 rounded papillae (Fig. 4B-5, 4D); mesothorax circumscribed anteriorly with verruciform sensilla (Fig. 4B-6); metathoracic lateral spiracular complex consists of a spiracle (Fig. 4E-1), a stelex sensillum (Fig. 4E-2), and two verruciform sensilla (Fig. 4E-3); abdominal lateral spiracular complex consists of a spiracle (Fig. 4F-1) and two verruciform sensilla (Fig. 4F-2); caudal segment circumscribed by minute acanthae; two stelex sensilla, dorsad and ventrad of posterior spiracular plates (Fig. 4G-1); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 4G-2); posterior spiracular plate bears three ovoid rimae, ca. 0.034 mm in length (Fig. 4G-3), and four interspiracular processes, each with 3–6 branches, longest measuring 0.018 mm (Fig. 4G-4); intermediate sensory complex (Fig. 4G-5), with a medusoid sensillum (Fig. 4H-1), and a stelex sensillum (Fig. 4H-2).

The third instar bears serrated rugose pads similar to the third instars of *T. imperfecta, T. jonesi, T. nigricornis, T. pseu-*

dovicina and *T. signata* (Goeden and Teerink 1997b, 1998; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1998). Compared to the second instar, the third instar bears only 3–5 papillae on the anterior spiracle. As with the high number of papillae in the second instar, so large a reduction in the number of papillae between instars has not been reported in any other *Trupanea* species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). These atypical characteristics call the identity of the second instars examined into question, but this stage was described from 10 replicates obtained from three different host species; which would reduce the probability that the same contaminent occurred in all four samples from which second instars were obtained.

The mesothorax alone is circumscribed by verruciform sensilla, similar to *T. nigricornis* (Knio et al. 1996a); whereas both the meso- and metathorax are circumscribed by verruciform sensilla in *T. arizonensis* and *T. imperfecta* (Goeden and Teerink 1998, Teerink and Goeden 1998). The third instar lateral spiracular complex is identical to that in *T. imperfecta* (Teerink and Goeden 1998). This is the first instance in which two species of *Trupanea* have shared the same type and number of sensilla in the metathoracic and abdominal lateral spiracular complexes (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Other pairs of congeneric species in other genera are known to share the same number and type of sensilla in the lateral spiracular complexes, e.g., *Procecidochares kristineae* and *P. lisae; Aciurina idahoensis* and *A. michaeli; A. thoracica* and *A. trixa* (Goeden and Teerink 1996a, b, 1997a; Headrick and Goeden 1993; Headrick et al. 1997).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae (Fig. 5C-1), two stelex sensilla dorsad and ventrad of posterior spiracular plates (Fig. 5C-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 5C-3); posterior spiracular plate bears three ovoid rimae (Fig. 5C-4), and four interspiracular processes, each with 3–6 branches (Fig. 5C-5); intermediate sensory complex with a medusoid sensillum and a stelex sensillum. Ninety-four puparia averaged 2.53 ± 0.03 (range, 1.71–3.17) mm in length; 1.24 ± 0.02 (range, 0.85–1.72) mm in width.

Distribution and Hosts

The distribution of *T. wheeleri* in North America north of Mexico as mapped by Foote et al. (1993) included Arizona, California, New Mexico, Oregon, Texas, and Utah in the western United States and a single record from near the border in adjacent western Canada.

Wasbauer (1972) and Goeden (1985, 1986, 1992) reported *T. wheeleri* from five tribes, 14 genera, and 29 species of host plants in North America. Five new rearing records for *T. wheeleri* are listed below in the manner of Goeden (1992), which along with taxonomic changes in Hickman (1993) and Goeden et al. (1998b), increase the reported host range to include seven tribes, 15 subtribes (Bremer 1994), 28 genera and 47 species. All flies were reared from ca. 1-liter samples of mature flower heads from California.

New host genera.—*Lasthenia, Machaeranthera, Psathyrotes, Senecio*

New host records.—*Erigeron aphanactis* (Gray) Greene, 3 ♂ and 1 ♀, SE of Mission Springs at 2480-m elevation, San Bernardino Nat. Forest (N section), San Bernardino Co., 17.vii.1997; *Lasthenia glabrata* Lindley, 1 ♂, San Jacinto Wildlife Area at 390 m, Lakeview, Riverside Co., 2.iv.1997; *Machaeranthera canescens* (Pursh) Gray, 1 ♂ and 1 ♀, N of Jenks Lake and S of Bar-

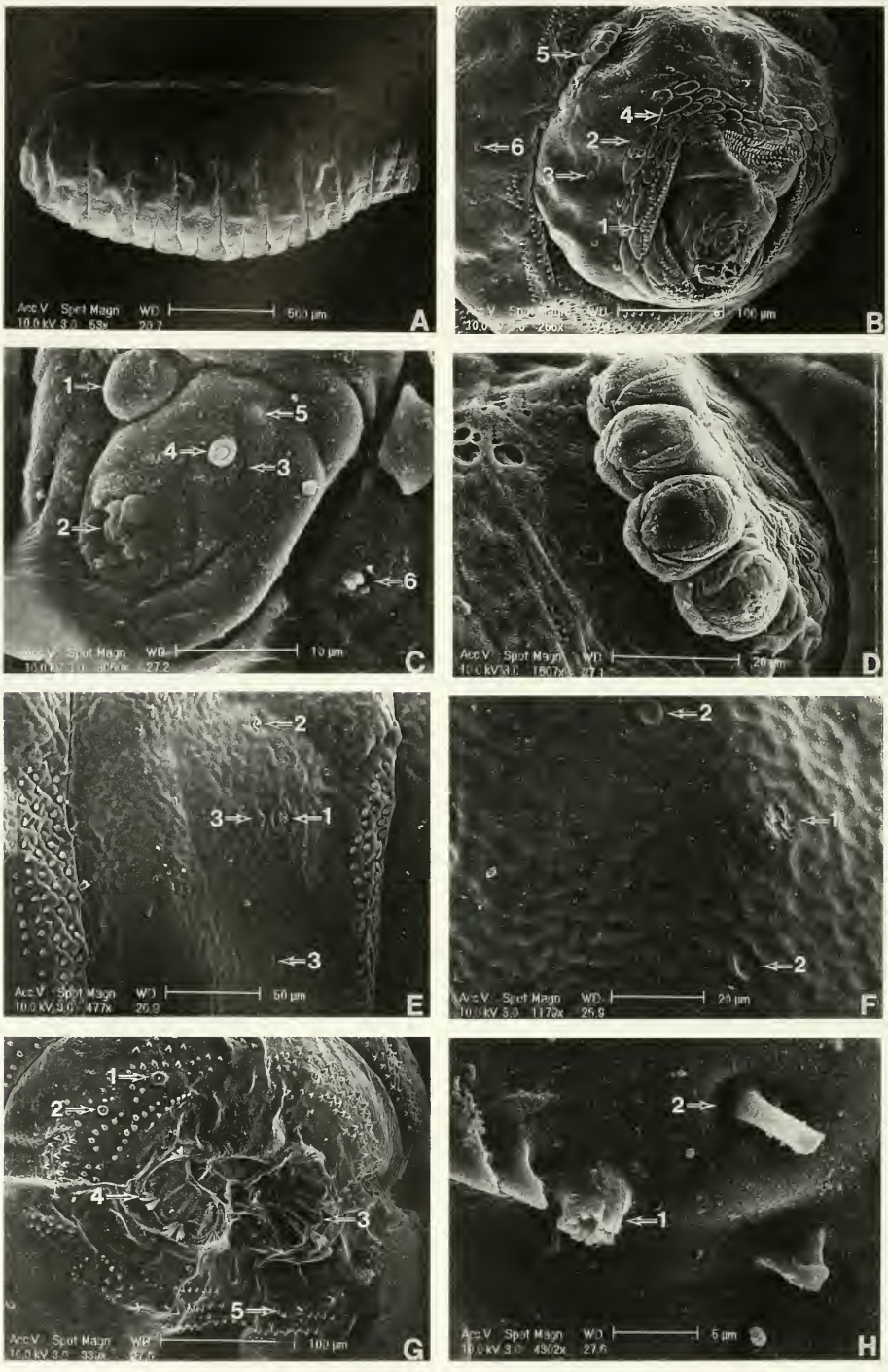

Fig. 4. Third instar of *Trupanea wheeleri:* (A) habitus, anterior to right; (B) gnathocephalon, prothorax, anteriolateral view, 1—minute acanthae, 2—rugose pad, 3—verruciform sensillum, 4—stelex sensillum, 5—anterior thoracic spiracle, 6—verruciform sensillum; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (D) anterior thoracic spiracle; (E) metathorax, 1—spiracle, 2—stelex sensillum, 3—verruciform sensilla; (F) first

ton Flats at 1830-m, San Bernardino Nat. Forest (N section), San Bernardino Co., 9.viii.1995; *Psathyrotes ramosissima* (Torrey) Gray, 2 ♀, Painted Canyon at 155 m, Riverside Co., 19.iii.1996; *Senecio canus* Hooker, 2 ♂ and 1 ♀, 1.6 km S of Beach Meadow at 2430 m, Sequoia Nat. Forest (N section), Tulare Co., 15.vii.1993.

All of the rearing records for the 45 reported hosts of *T. wheeleri* are from California, and all but four of these were confirmed by us or are ours or RDG's records, including nine recently reassigned from *T. actinobola* (Goeden et al. 1998b). Of the eight valid host names that Wasbauer (1972) listed, we have confirmed four. As known to date, most hosts for *T. wheeleri* belong to the tribe Astereae (26 spp.), with good representation from the Helenieae (9 spp.) and Heliantheae (4 spp.), and token representation from Eupatorieae (2 spp.), Senecioneae (2 spp.), Anthemideae (1 sp.), and Mutiseae (1 sp.) (Munz 1974, Hickman 1993, Bremer 1994). Similarly, the subtribe Solidagininae (21 spp.) is best represented, with additional representation in the subtribes Asterinae (5 spp.), Verbesininae (3 spp.), Alomiinae (2 spp.), Baeriinae (2 spp.), Chaenactidinae (2 spp.), Madiinae (2 spp.), Achilleinae (1 sp.), Gaillarediinae (1 sp.), Nassauviinae (1 sp.), Pectidinae (1 sp.), Peritylinae (1 sp.), Senecioninae (1 sp.), Tussilagininae (1 sp.) (Bremer 1994).

Biology

Trupanea wheeleri is a difficult species to study in flower heads because it usually co-occurs with other tephritids in the same host-plant species (symphagy) (Goeden 1997), including congeners, and only certain host species sampled at certain locations contained mixes of immature stages of recognizable species.

Egg.—A total of 27 eggs was recovered from preblossom flower heads of *Corethrogyne filaginifolia* (Hooker and Arnott) Nuttall, *Ericameria brachylepis* (A. Gray) H. M. Hall (=*Haplopappus propinquus* S. F. Blake) and *Hazardia* (formerly *Haplopappus*) *squarrosus* (Hooker and Arnott) Greene, for an average of 2.5 ± 0.2 (range, 1–4) eggs per flower head. All eggs were inserted pedicel-last, mostly through the phyllaries or between their appressed apices, perpendicular to or at 30° to 60° to the receptacle, and alongside or into a corolla or ovule of a floret on the periphery or at the center of a closed, immature flower head (Fig. 6A, B). Most eggs were oviposited singly (Fig. 6A, B) or side-by-side, in pairs, or rarely, in threes by single females.

Larva.—Upon eclosion, first instars tunneled into and fed mainly on corollas of florets and on ovules in preblossom flower heads. No receptacle within flower heads was pitted by first-instar feeding in a total of 10 heads of *E. brachylepis* and *H. squarrosus* (Fig. 6C).

Second instars fed mainly on ovules and florets of preblossom flower heads and soft achenes of open flower heads (Fig. 6D). Receptacles of a total of 13 flower heads of *C. filaginifolia, Ericameria palmeri* (Gray) Hall, and *H. squarrosus* containing second instars averaged 1.9 ± 0.3 (range, 0.9–3.7) mm in diameter and none was pitted. These flower heads contained an average of 1.7 ± 0.2 (range, 1–3) second instars that had fed upon an average of 5.3 ± 0.7 (range, 3–10) florets/ovules/achenes, or 31% (range, 9–67%) of an average total of 21 ± 4.0 (range, 8–58) florets/ovules/achenes per head.

Third instars fed on soft achenes at the centers, and less commonly to the margins, of open or postblossom flower heads (Fig.

←

abdominal segment, 1—spiracle, 2—verruciform sensilla; (G) caudal segment, 1—stelex sensillum, 2—verruciform sensillum, 3—rima, 4—interspiracular process, 5—intermediate sensory complex; (H) intermediate sensory complex, 1—medusoid sensillum, 2—stelex sensillum.

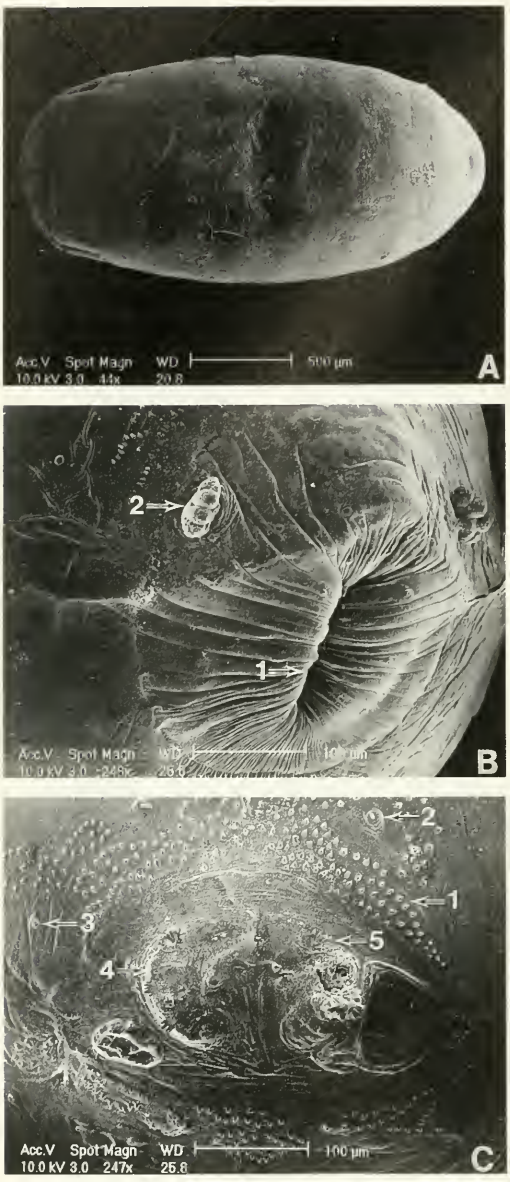

Fig. 5. Puparium of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—minute acanthae, 2—stelex sensillum, 3—verruciform sensillum, 4—rima, 5—interspiracular process.

6E, F). In a total of 28 flower heads of *Acourtia* (formerly *Perezia*) *microcephala* deCandolle, *C. filaginifolia, E. palmeri,* and *H. squarrosus* averaging 1.8 ± 0.1 (range, 1.1–2.6) mm in diameter and containing an average of 1.4 ± 0.1 (range, 1–4) third instars and 18.8 ± 1.9 (range, 6–36) achenes, an average of 6.8 ± 1.0 (range 1–23) soft achenes were damaged. Most third instars fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles, within the upper parts of the soft achenes, and well above the receptacles (Fig. 6E). Consequently, only three (11%) receptacles of flower heads that respectively contained three, two, and one third instars were pitted in the 28 flower heads examined. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 6F).

Pupa.—As noted with other florivorous, congeneric tephritids studied (Goeden and Teerink 1998, 1999; Goeden et al. 1998a, b), flower heads containing puparia (Fig. 6G) had the greatest amount of damage that the seed-feeding larvae of *T. wheeleri* caused within flower heads sampled. The receptacles of 90 infested, blossom and postblossom flower heads of *A. microcephala, C. filaginifolia, E. palmeri,* and *H. squarrosus* containing puparia averaged 1.7 ± 0.1 (range, 0.9–2.9) mm in diameter and bore an average of 15.2 ± 1.1 (7–32) soft achenes, of which an average of 6.9 ± 0.6 (range, 1–16) soft achenes or 45% (range, 19–100%) were damaged. About half of the receptacles were pitted and about half of the puparia were found next to the phyllaries at the margins of flower heads; the remaining flower heads contained puparia at or near their centers (Fig. 6G). All puparia had their anterior ends facing away from the receptacles, and their long axes were perpendicular to the receptacles (Fig. 6G).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 20 unmated males (Fig. 6H, I) averaged 91 ± 11 (range, 32–230) days, and 23 virgin females (Fig. 6H) averaged 68 ± 8 (range, 21–181) days. Like *T. actinobola, T. arizonensis, T. jonesi,* and *T. pseudovicina* (Goeden and Teerink 1998, 1999; Goeden et al. 1998a, b), these flies

Fig. 6. Life stages of *Trupanea wheeleri:* (A) egg inserted in corolla of floret of *Machaeranthera canescens*; (B) egg inserted in corolla of floret of *Corethrogyne filaginifolia*; (C) first instar in ovules in flower head of *M. canescens*; (D) second instar tunneling in ovules in flower head of *C. filaginifolia*; (E) third instar in center of open flower head of *C. filaginifolia*; (F) late third instar in center of open flower head of *Erigeron foliosus* Nuttall; (G) puparium in flower head of *Erigeron foliosus*; (H) mating pair, ventral view; (I) mating pair, side view. Lines = 1 mm.

are among the longer average and maximum adult longevities that we have recorded for native species of nonfrugivorous Tephritidae from southern California. Such lengthy longevities are consistent with the aggregative type of life cycle ascribed below to this tephritid.

The premating and mating behaviors of *T. wheeleri* were briefly studied in the laboratory; however, the petri dish arenas found to be so useful with many other Tephritinae species (Headrick and Goeden 1994), but unsatisfactory with most *Trupanea,* facilitated only two matings of 5 and 7 minutes duration each observed between 14:00 and 15:00 h PDST (Fig. 6H, I). See Headrick and Goeden (1994), Knio et al. (1996b), Goeden et al. (1998a, b) for descriptions of premating and mating behaviors of congeneric California species.

Seasonal history.—The life cycle of *T. wheeleri* in southern California follows an aggregative pattern in which the long-lived adults in reproductive diapause overwinter and aggregate to mate on preblossom host plants in the spring (March–April) (Headrick and Goeden 1994). They reproduce first in the Colorado Desert, then in the higher-elevation Mojave Desert, interior valleys, and coastal areas (Headrick and Goeden 1994). Like *T. jonesi* (Goeden et al. 1998a) and *T. nigricornis* (Knio et al. 1996b), reproduction by subsequent generations of these multivoltine tephritids continue thereafter throughout the spring, summer, and fall on a wide range of alternate host plants, as flowering of Asteraceae continues at ever higher elevations and more northerly latitudes in California.

Natural enemies.—Seven species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. wheeleri* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma* n. sp.? (Eurytomidae), *Eurytoma obtusiventris* Gahan (Eurytomidae), *Eurytoma veronia* Bugbee (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Mesopolobus* sp. (Pteromalidae), *Pteromalus* sp. (Pteromalidae), *Torymus* sp. (Torymidae).

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TWO NEW SPECIES OF *APHIS* L. (HEMIPTERA: APHIDIDAE) FROM ARGENTINA LIVING ON ASTERACEAE

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Abstract.—Two new Argentinean aphid species are described: ***Aphis* (*Aphis*) *coridifoliae*,** living on *Baccharis coridifolia* from Cordoba Province, and ***Aphis* (*Aphis*) *melosae*,** living on *Grindelia chiloensis* from Mendoza Province. The apterous and alate viviparous females of both species are described, and two forms of *A.* (*A.*) *melosae* apterae are distinguished: "big" and "dwarf." The differences between the new species and other closely related species are given.

Resumen.—"Dos nuevas especies de *Aphis* (Hemiptera: Aphididae) propias de Asteraceae de Argentina". Se decriben las hembras vivíparas ápteras y aladas de dos nuevas especies de pulgones de Argentina: ***Aphis* (*A.*) *coridifoliae*,** de la provincia de Córdoba, sobre *Baccharis coridifolia,* y ***Aphis* (*A.*) *melosae*,** de la provincia de Mendoza, sobre *Grindelia chiloensis.* Se distinguen dos tipos de vivíparas ápteras de *A.* (*A.*) *melosae:* las grandes y las enanas. Se discuten las diferencias entre las nuevas especies y otras próximas.

Key Words: aphid, new species, pulgón, especie nueva

The genus *Aphis* Linnaeus, 1758 and its nominotypical subgenus are the largest genus and subgenus of Aphididae (Remaudière and Remaudière 1997), and they are mostly distributed in the northern territories.

There are few *Aphis* s. st. species recorded in the southern territories of the World: 8 in Australia (Eastop 1966), 16 in Sub-Saharan Africa (Millar 1994), approximately 29 in India (Ghosh 1975, 1977, Raychaudhuri, Ghosh and Basu 1980) although Numann-Etienne and Remaudière (1995) recorded seven species in Pakistan, which are not known in India.

In South America 25 species of the subgenus *Aphis* are known (and two species of the subgenus *Protaphis* Börner, 1952) (Ortego and Mier Durante 1997). This number may increase, because of the presence of large areas with favorable climatic conditions for this subgenus, especially the southern part of South America. Moreover, a high proportion of recorded species there are endemic: 11/25 species (Remaudière 1994, Ortego and Mier Durante 1997).

Four *Aphis* s. st. species live on Asteraceae in South America: *Aphis coreopsidis* (Thomas 1878) is also known in North America and Africa, *A. helianthi* (Monell 1879) is also known in North America, and two endemic species *A. senecionicoides*

Blanchard 1944 and *Aphis* sp. unpublished (Ortego 1998). Moreover the polyphagous and more or less cosmopolitan *A. craccivora* Koch, 1854, *A. fabae* Scopoli, 1763, and *A. spiraecola* Patch, 1914, can live on Asteraceae, and, in fact, they have been recorded on Asteraceae in South America.

Two new species of *Aphis* s. st. have been found in Argentina on the South American Asteraceae *Grindelia* and *Baccharis,* and these are described here.

Abbreviations used in the text and tables are as follows: abd.seg.I to VIII = abdominal segment I to VIII; ant.III, IV, V = antennal segments III, IV, V; ant.VIb and ant.VIpt = base and processus terminalis of antennal segment VI; BL = body length; D = basal diameter of ant.III; d = diameter of trochanter-femoral joint of hind legs; h.t.II = second segment of hind tarsus; u.r.s. = ultimate rostral segment. Values in parentheses () are exceptional values.

Aphis (*A.*) *coridifoliae* Mier Durante and Ortego, new species

(Fig. 1)

Apterous viviparous female (n = 142; 16 measured) (Fig. 1A–I).—Body 1.00 to 1.70 mm. long, 7.38 to 10.00 (mostly 8 to 9) times siphunculus. Light or greenish yellow when alive, with white waxy powder, reticulated, with apex of antenna and legs, siphunculus and cauda dark brown to black and frequently with lateral dark brown spots on abdomen (intersegmental sclerites). Prepared specimens light in general with head, most of antenna and legs, rostrum and sometimes postsiphuncular, and dorso-abdominal VII and VIII sclerites (paler), smoky, and apex of ant.V, antennal segment VI, apex of tibiae, tarsi, sometimes apex of hind femur III, intersegmental sclerites, siphunculus, cauda and genital and anal plates dark brown to black.

Dorsal cuticle slightly and irregularly reticulated. Setae pale, short (Table 1), acute or dorsal ones slightly blunt. Large and low domelike marginal papillae on prothorax (bigger) and abd.seg.I and VII (exceptionally absent on abd.seg.VII); 2 to 7 (frequently 4 to 6) marginal papillae similar in shape, but smaller, on abd.seg.II, III, IV and VI.

Frontal profile convex, slightly sinuate. Antenna 5 or 6 segmented (without correspondence with BL), (0.57) 0.62 to 0.90 mm, (0.42) 0.480 to 0.59 times BL; antennal segment lengths (in mm): ant.III+IV (5 segmented antenna) = 0.21 to 0.33; ant.III (6 segmented antenna) = 0.10 to 0.25; ant.IV (also 6 segmented) = 0.07 to 0.14; ant.V = 0.08 to 0.15; ant.VIb = 0.08 to 0.12; ant.VIpt = 0.10 to 0.14; ant.III 1.87 to 2.95 (5 segmented antenna) or 0.87 to 1.79 (6 segmented antenna) times longer than ant.VIpt, which is (0.91) 1.14 to 1.47 times longer than ant.VIb. Antennal setae few: 2 to 4 (6) and 1 to 3 respectively on ant.III and IV (6 segmented antenna) or on their correspondent parts (5 segmented antenna).

Rostrum (0.33 to 0.40 mm long) reaching hind coxae; BL. 3.03 to 4.56 times length of rostrum; u.r.s. 0.09 to 0.11 mm long, 2.0 to 2.5 (2.7) times as long as its basal width, 0.95 to 1.11 longer than h.t.II, (0.92) 1.00 to 1.25 times ant.VIb, with sides slightly concave and 2 accessory lateral setae.

Hind tibia (0.32) 0.37 to 0.44 times BL. First tarsal segment with 3.3.2. setae, as is normal in *Aphis* (Eastop 1966); h.t.II 0.09 to 0.11 mm long.

Conspicuous intersegmental sclerites; a narrow bar across dorsum of abd.seg.VIII in front of setae and sometimes small spinal on abd.seg.VII and sometimes postsiphuncular sclerites. Abd.seg.I to VI with 2 (rarely 3) marginal setae each side and 2 spinal ones; only two setae on abd.seg.VIII. Siphunculus more or less cylindrical, slowly enlarged on basal third, rough, 0.11 to 0.22 mm long, 2.80 to 4.00 times its width in middle, and 0.89 to 1.26 times cauda. Subgenital plate with 2 anterior and 4–10 posterior setae. Cauda fingerlike, 0.12 to 0.18

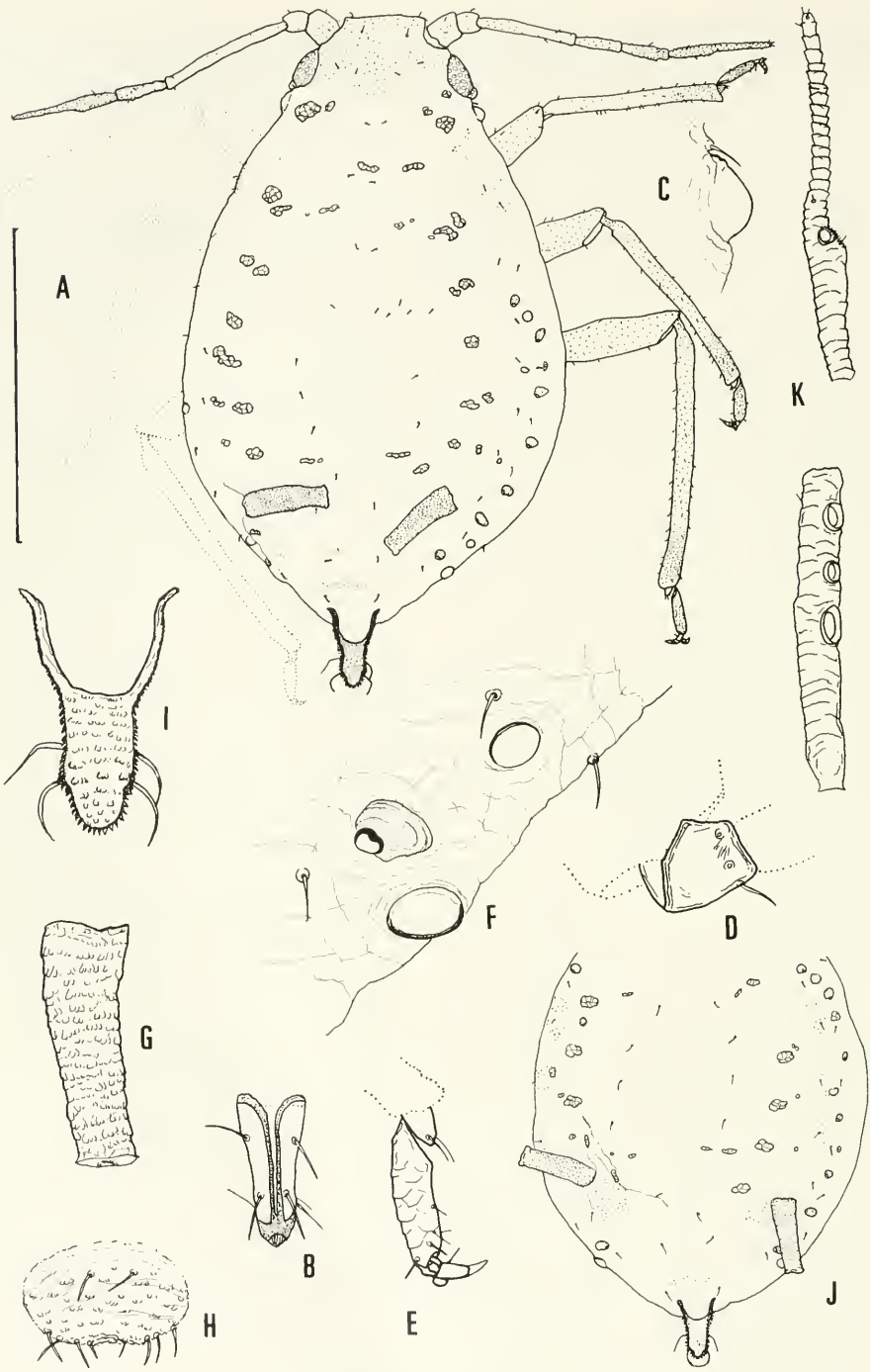

Fig. 1. *Aphis* (*A.*) *coridifoliae*. A–I, Apterous viviparous female. J–K, Alate viviparous female. A, Habitus. B, Ultimate rostral segment. C, Prothoracic marginal papillae. D, Hind trochanter. E, Hind tarsus. F, Marginal part of the abd.seg.VI and VII. G, Siphunculus. H, Subgenital plate. I, Cauda. J, Abdomen. K, Antennal segments III (above) and VI. Scale bar = 0.615 mm (A, J), 0,40 mm (H), 0,20 (B, D, E, G, I, K), 0,125 mm (C, F). Illustrations by María Nieto González.

Table 1. Setae measurements of *Aphis* (*A.*) *coridifoliae*, apterous viviparous [ap. viv.] and alatae viviparous [al. viv.] females.

		ap. viv.	al. viv.
ant.III	µm long	7–13	10–13
	D times	0.5–0.9	0.8–1.0
vertex	µm long	10–18	13
	D times	0.7–1.4	0.9–1.0
hind trochanter	µm long	22–30	20–25
	d times	0.5–0.8	0.6–0.8
hind femur: dorsal	µm long	10–18	10–13
	D times	0.7–1.4	0.8–1.0
abd.seg.III: spinal	µm long	15–20	12–18
	D times	0.9–1.6	1.0–1.4
abd.seg.III: marginal	µm long	10–20	12–18
	D times	0.7–1.4	1.0–1.4
abd.seg.VII: spinal	µm long	17–28	20–28
	D times	1.2–2.2	1.6–2.2
abd.seg.VIII	µm long	20–30	22–28
	D times	1.5–2.4	1.8–2.2

mm long, 1.19 to 1.52 times its basal width, with 4 to 6 setae.

Alate viviparous female (n = 8; 5 measured) (Fig. 1J, K).—Body 1.22 to 1.48 mm long. Alive and mounted similar to apterae, but darker on head, antenna (ant.I, ⅔ distal ant.III, ½ distal ant.V and VI dark; ant.II, other parts of ant.III and V and ant.IV smoky), thorax and legs (excepted basal ⅔ of tibiae). Four to eight large and rounded secondary sensoria on ant.III. Marginal sclerites on abd.seg.II to IV present; other dorsal sclerites on abdomen also similar to those in apterae.

Other metric and meristic characters (setae included, Table 1) very similar to apterae, but with following differences: ant.III up to 0.235 mm length and 1.48 to 2.24 times ant.VIpt, siphunculus (narrower than apterae) 3.14 to 3.75 times its medial width, and cauda 1.05 to 1.55 its basal width.

Type material.—Holotype: apterous viviparous female (measured specimen number 16) collected on *Baccharis coridifolia* DC at Villa Dolores (Córdoba province, Argentina; 32°00′S, 65°10′W, 540 m), 1-XI-96, J. Ortego leg., in collection Universidad de León (Departamento de Biología Animal). Paratypes: 141 apterous and 8 alate viviparous females found (J. Ortego leg.) on the same host-plant at the same locality, 3-IX-95 and 1-XI-96, deposited in the authors' collections (Universidad de León, and INTA-Malargüe) and in The Natural History Museum, London and Muséum National d'Histoire Naturelle, Paris.

Etymology.—The specific name is an adjective used as a substantive in the genitive case derived from the specific name of the aphid's hostplant: *coridifolia* (I.C.Z.N., article 11 (h) (i) (4), International Commision of Zoological Nomenclature 1985).

Biology and distribution.—*Aphis* (*A.*) *coridifoliae* is possibly monoecious and holocyclic on *Baccharis coridifolia* and perhaps on other related species of *Baccharis* (Asteraceae). It forms small and dense colonies on the stems of the host plant, which is distributed, from the center of Argentina to Bolivia, Paraguay and southern Brazil; these territories constitute the potential area of distribution of the new aphid species.

Discussion.—*Aphis* (*A.*) *baccharicola* Hille Ris Lambers, 1974 is the only other *Aphis* species specific on *Baccharis*; it lives on *Baccharis pilularis* DC. in California (U.S.A.). It belongs to the *Aphis helianthi* Monell group (Hille Ris Lambers 1974), and it is a very different species from *A.* (*A.*) *coridifoliae*. Apterous viviparous females of *A.* (*A.*) *baccharicola* have marginal sclerites, have not marginal papillae on abd.II to VI, and have longer setae (50–60 µm and 70 µm on abd.seg. III and VIII respectively, and setae on ant.seg.III twice as long as D) longer ant.VIpt, and longer siphunculus, which frequently have setae.

Aphis (*A.*) *coridifoliae* can be differentiated from the majority of species in the subgenus *Aphis* recorded in South America, by the short ant.VIpt (1.47 times ant.VIb at most) in both apterous and alate viviparous females.

The ant.VIpt is shorter than 1.5 times ant.VIb only in *A.* (*A.*) *danielae* Remaudière, 1994, *A.* (*A.*) *mulinicola* Hille Ris Lambers, 1974 and *A.* (*A.*) *senecionicoides*

Blanchard, 1944. In *A.* (*A.*) *danielae* apterous viviparous females, living on *Lycium* sp. (Solanaceae), the marginal papillae on abd.seg.II to VI are absent, the u.r.s. is relatively long (at least 0.11 mm) and the discal plate on the abdomen is frequently present. In *A.* (*A.*) *mulinicola* apterous viviparous females, living on *Mulinum* (Apiaceae), the discal plate on the abdomen is present and the cauda has 8–10 setae. In *A.* (*A.*) *senecionicoides* apterous viviparous females, living on *Senecio* (Asteraceae), the marginal papillae on abd.seg. II to VI are absent and the u.r.s. is longer (approximately 0.16 mm).

Sometimes, the apterous and alatae females of *Aphis* (*A.*) *schinifoliae* Blanchard, 1939 and the apterous females of *A.* (*A.*) *craccivora* Koch, 1854, have the ant.VIpt shorter than 1.5 times ant.VIb. *A.* (*A.*) *schinifoliae* apterae have light and outwardly curved siphunculi and lack marginal papillae on abd.seg.II to VI and *A.* (*A.*) *craccivora* apterae have a discal plate on the abdomen and 3 marginal papillae on abd.seg.II to VI at most. *Aphis schinifoliae* lives on *Schinus* spp. (Anacardiaceae) and *A. craccivora* is polyphagous.

Aphis (*A.*) *melosae* Mier Durante and Ortego, new species

(Fig. 2)

Apterous viviparous female (n = 301; 34 measured) (Fig. 2A–K).—Two forms are distinguished (1) "big" ones: BL = (1.45) 1.52 to 2.05 mm, dark brown to blackish brown; shining, with abdominal plate and mainly with secondary sensoria on ant.III, and (2) "dwarf" ones: BL = 0.97 to 1.45 mm, light brown to dark green, more or less opaque, with an incomplete or without abdominal plate and without secondary sensoria.

Mounted specimens "big" are dusky light in general, with head, ant.I, II, V (apex) and VI, rostrum, coxae, dorsal part of hind femur (sometimes also front and middle femora) and dorsal plates smoky to light brown, apex of tibiae, tarsi, siphunculus (darkest), cauda and anal and genital plates dark brown to black; "dwarf" specimens with ant.II and V and femora, paler than "big" ones.

Dorsal cuticle more or less reticulated. Setae hard, acute and pale (measurements in Table 2). Marginal papillae present on prothorax and abd.seg.I and VII, elevated domelike to ovoidal in shape but different in size, prothoracic ones are largest and ones on abd.seg.VII are smallest and sometimes absent in "dwarf" specimens; (1) 3 to 6 ("big" specimens) or 0 to 2 (5) ("dwarf") marginal papillae in all on abd.seg.II, III and IV.

Front moderately sinuate, with shallow laterofrontal sinuses. Antenna 6 ("big" and "dwarf") or 5 ("dwarf") segmented; 0.92 to 1.25 ("big") or 0.55 to 0.90 ("dwarf") mm long and 0.52 to 0.67 times BL, measurements of antennal segments on Table 3; antennal setae few: 5 to 8 (12) ("big") or 2 to 8 ("dwarf") on ant.seg.III (6 segmented antenna) or on its correspondent part (5 segmented antenna). "Big" specimens with 0 to 6 rounded secondary sensoria, placed on line on ant.III; sensoria per antenna (34 antennae examined)—0: 26% antennae, 1–3: 50% and 4–6: 24%.

In "big" specimens rostrum reaching hind coxae, it is 0.50 to 0.65 mm long and 0.28 to 0.41 times BL; and u.r.s. is 0.14 to 0.17 mm long, 2.07 to 3.33 times as long as its basal width and 1.11 to 1.32 longer than h.t.II. In "dwarf" specimens rostrum reaching up to abd.seg.V, it is 0.44 to 0.57 mm long and 0.34 to 0.47 times BL; and u.r.s. is 0.11 to 0.14 mm long, 2.25 to 3.00 times as long its basal width and 1.20 to 1.37 h.t.II. In both kinds, u.r.s. with sides slightly concave and 2 accessory lateral setae.

Hind tibia 0.43 to 0.58 times BL. First tarsal segment with 3.3.2 setae; h.t.II 0.09 ("dwarf") or 0.11 ("big") to 0.14 mm long.

Abdomen of "big" specimens with a spino-pleural plate from mesothorax to

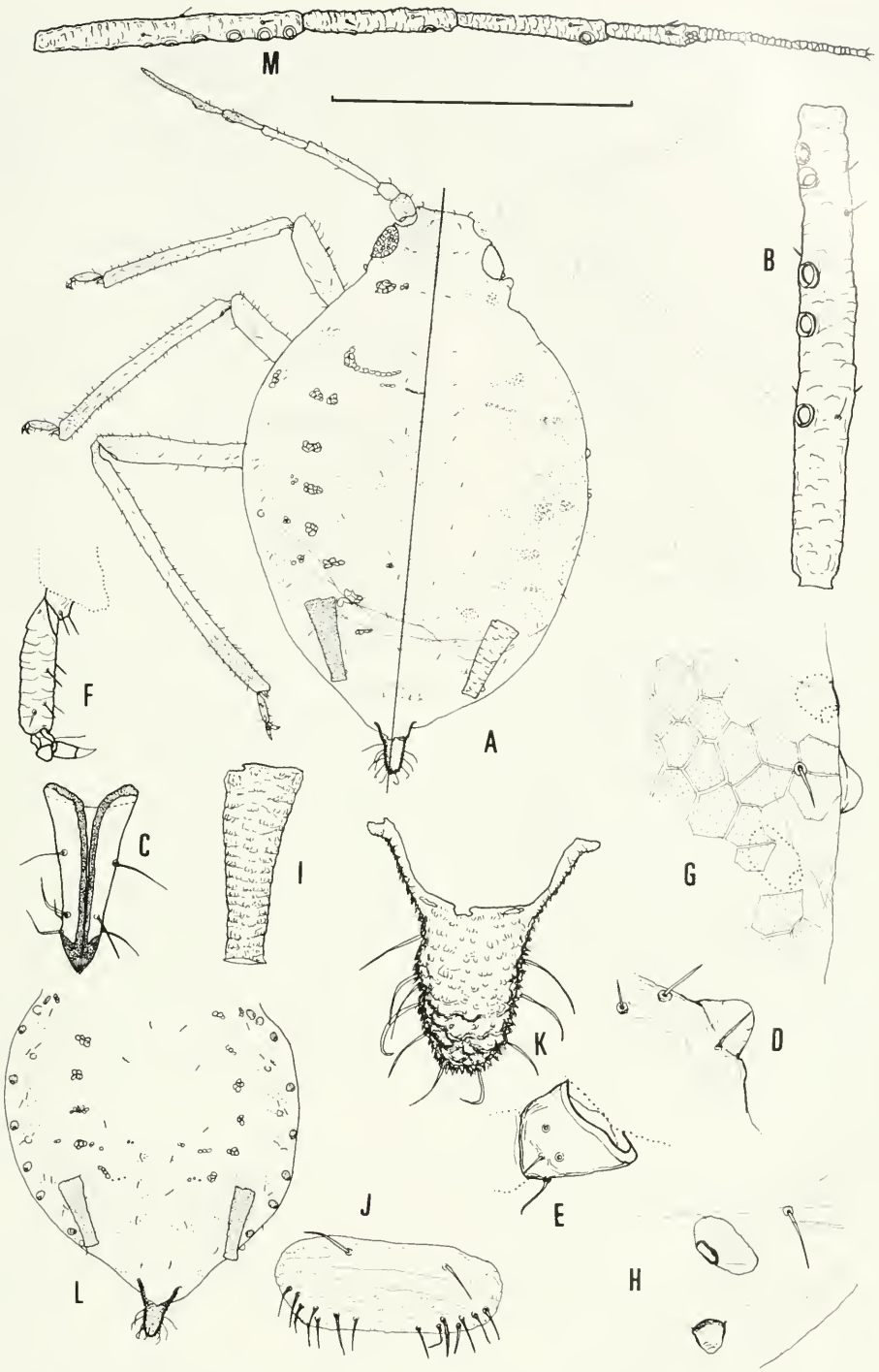

Fig. 2 *Aphis* (*A.*) *melosae*. A–K, Apterous viviparous female "big." L–M, Alate viviparous female. A, Habitus (on left with pigmentation, on right without pigmentation). B, Antennal segment III. C, Ultimate rostral segment. D, Prothoracic marginal papillae. E, Hind trochanter. F, Hind tarsus. G, Marginal part of abd.seg.I. H, Marginal part of abd.seg. VII. I, Siphunculus. J, Subgenital plate. K, Cauda. L, Abdomen. M, antennal flagellum. Scale bar = 1 mm (A, L), 0.40 mm (I, J, M), 0.27 mm (E), 0.25 mm (C, F), 0.20 mm (B, D, G, H, K). Illustrations by María Nieto González.

Table 2. Setae measurements of *Aphis* (*A.*) *melosae* apterous viviparous [ap. viv.] "big" and "dwarf" and alatae viviparous [al. viv.] females.

		ap. viv.		
		"big"	"dwarf"	al. viv
ant.III	µm long	15–25	10–23	15–23
	D times	0.7–1.4	0.6–1.3	0.8–1.2
vertex	µm long	25–33	20–30	25–35
	D times	1.3–2.0	1.3–2.2	1.1–2.0
hind trocanter	µm long	30–43	25–40	27–37
	d times	0.5–0.8	0.6–0.9	0.5–0.7
hind femur: dorsal	µm long	25–40	15–25	20–28
	D times	1.1–2.0	1.0–2.0	1.1–1.5
abd.seg.III: spinal	µm long	22–33	17–30	20–33
	D times	1.1–2.0	1.1–2.0	1.1–1.9
marginal	µm long	25–38	17–30	22–33
	D times	1.1–2.2	1.1–2.2	1.2–2.0
abd.seg.VII: spinal	µm long	30–43	22–38	20–40
	D times	1.5–2.3	1.6–2.6	1.1–2.3
abd.seg.VIII	µm long	30–45	25–38	32–43
	D times	1.7–2.5	1.8–3.0	1.8–2.8

abd.seg.IV or V (from prothorax to abd.seg.VI in early spring) more or less coalescents with marginal sclerites (mostly independent) and frequently with intersegmental breaks; a transverse bar with different degree of development on posterior segments. Abdomen of "dwarf" specimens at most with marginal sclerites, a lobulated spino-pleural plate from mesothorax to abd.seg. IV (frequently fragmented) and a narrow transversal bar on posterior segments; but sometimes only several small marginal sclerites and a bar on abd.seg.VIII. Two (exceptionally 1, 3 or 4) setae on abd.seg.VIII and 2 marginal setae at each side on presiphuncular abdominal segments.

Siphunculus more or less cylindrical or slowly cone-truncated, rough, in "big" specimens 0.20 to 0.33 mm long (2.32) 3.42 to 4.71 (5.46) longer its width at middle and 1.26 to 1.65 times the cauda, in "dwarf" specimens 0.09 to 0.20 mm long, (2.22) 2.60 to 4.00 (4.34) longer than its width and 0.95 to 1.18 (1.39) times the cauda. Subgenital plate with 2 anterior setae and 10–17 ("big") or 8–13 ("dwarf") posterior setae. Cauda broad fingerlike, in "big" specimens 0.15 to 0.21 mm long, 1.00 to 1.21 (1.38) times its basal width and

Table 3. Antennal segments measurements of *Aphis* (*A.*) *melosae* apterous viviparous [ap. viv.] "big" and "dwarf" and alatae viviparous [al. viv.] females.

	ap. viv. "big"	ap. viv. "dwarf"		al. viv.
	6 segmented	6 segmented	5 segmented	6 segmented
ant.III (mm)	0.25–0.36	0.14–0.22	0.17–0.35	0.25–0.37
ant.IV (mm)	0.11–0.22	0.06–0.12		0.13–0.23
ant.V (mm)	0.14–0.18	0.06–0.14	0.07–0.13	0.13–0.21
ant.VIb (mm)	0.09–0.12	0.08–0.11	0.07–0.10	0.09–0.12
ant.VIpt (mm)	(0.18) 0.21–0.26	0.14–0.20	0.14–0.20	0.20–0.24
ant.III/ant.VI..pt.	1.21–1.68	0.91–1.43	1.17–1.75	1.19–1.64
ant.VIpt/ant.VIb	(1.76) 2.00–2.35	(1.40) 1.70–2.00	1.87–2.18	1.82–2.33
u.r.s./ant.VIb	1.30–1.53	1.28–1.53	1.35–1.60	1.16–1.50

with 8 to 12 setae, and in "dwarf" specimens 0.08 to 0.14 mm long, 0.86 to 1.10 (1.25) times its basal width and with 6 to 10 setae.

Alate viviparous female (n = 63; 13 measured) (Fig. 2L, M).—Body 1.35 to 2.02 mm long. When alive, brown with head, thorax, antenna (2/10 basal part of ant.III, up to ½ basal part of ant.IV, and ant.V, dusky), legs (nearly all femur I, ⅓ base of femur III and ¾ base of tibiae pale to smoky), abdominal bars, siphunculus and cauda dark brown to black.

Abdomen with marginal presiphuncular and postsiphuncular sclerites, specially developed intersegmental sclerites abd.seg.IV–V, isolated sclerites or spinal bar on abd.seg.VI, a wide bar on ant.seg.VII, and 2 isolated sclerites or a bar on abd.seg.VIII. Setae similar to those of apterae (Table 2). Marginal papillae similar in size and shape to those of apterae; some specimens without one or both papillae on abd.seg.VII; 1 to 6 ones on abd.seg.II to abd.seg.IV.

Antenna 6 segmented, 0.90 to 1.28 mm long and 0.58 to 0.76 times BL; measurements of antennal segments in Table 3. Ant.III with 7 to 13 secondary sensoria (sensoria per antenna (26 antennae examined)—7–8: 54% antennae, 9–10: 31% and 11–13: 15%), ant.IV with 0 to 4 and ant.V very exceptionally with 1 or 2 (1 on one antenna of 2 specimens and one per antenna in one specimen). U.r.s.= 0.13 to 0.16 mm long, 1.87 to 3.00 its basal width and 1.12 to 1.33 times h.t.II.

Siphunculus 0.13 to 0.27 mm long, 3.25 to 5.40 its width in the middle and 1.19 to 1.43 times the cauda. Subgenital plate with 2 or 3 (exceptionally 4) anterior setae and 8 to 15 posterior ones. Cauda similar in shape to those apterae, 0.10 to 0.19 mm long, 0.91 to 1.34 times its basal width and with 8–11 (15) setae.

Type material.—Holotype: apterous viviparous female "big" (measured specimen number 2) collected on *Grindelia chiloensis* (Corn.) Cabrera at Malargüe (Mendoza province, Argentina, 35°00′S, 69°25′W, 1,400 m), 28-X-94, J. Ortego leg. in collection Universidad de León (Departamento de Biología Animal). Paratypes: 300 apterous and 63 alate viviparous females found (J. Ortego leg.) on the same host-plant at the same locality on 17-XI-93, 28-X-94, 6-XII-94, 25-XI-95, 28-III-96, deposited in the author's collections (Universidad de León and INTA Malargüe) and in The Natural History Museum, London and Muséum Nationale d'Histoire Naturelle, Paris.

Etymology.—The specific name is a noun in the genitive case derived from the common (Spanish) name of the aphid's host-plant: "melosa" (I.C.Z.N., article 11 (h) (i) (3), International Commision of Zoological Nomenclature 1985).

Biology and distribution.—*Aphis(A.) melosae* is monoecious on the Asteraceae *Grindelia* spp., mainly *G. chiloensis* (Cornel.) Cabrera but also on *G. tehuelches* (Speg.) Cabrera ("La Cruz Negra", Tupungato, Mendoza, Argentina, 21-XI-97, J. Ortego leg.) and perhaps on other related species of this genus. It forms dense colonies on the stems and the axil of leaves ("big" and "dwarf") and on the underside of the leaves ("dwarf") of its host plant.

The "big" specimens are present from early spring (at the end of September) to the end of spring, and also in autumn (specimens found on 19-IV-96). The "dwarf" specimens appear in November and they have been found until March or April. It is evident that the "dwarf" form is a summer dwarf form (Miyazaki 1987), as in other *Aphis* spp., for example *A. urticata* Gmelin, 1790 or *A. ruborum* (Börner, 1932) in Europe and *A. gossypii* Glover, 1877 around the World.

The alate viviparous females coexist with the "big" apterous females, but we have not found alatae with the "dwarf" ones. We have not found sexual forms. It is possible that the species is holocyclic, but it is more probable that it is anholocyclic because the characteristics of its host-plant during the winter permit aphids to live protected.

The new species is possibly distributed

in dry areas of the southern half of Argentina, because *Grindelia chiloensis* is distributed on sandy or rocky dry areas of the central western part of Argentina and *G. tehuelches* reaches south to Santa Cruz province.

Discussion.—*Aphis melosae* is a very good example of the variability in aphids. There are several important differences between the apterous viviparous females named by us as "big" and "dwarf". These differences are so significant that it would be possible to think that two species are involved, but the coexistence of two kinds of apterous females in November, December and April and the characteristics of the alate females (Tables 2–3) allow us to affirm that only one species is involved.

Aphis melosae belongs to the "*craccivora*" or "*Pergandeida*" species group, characterised by the presence of a more or less developed thoracico-abdominal or abdominal discal plate. Although *A. craccivora* is polyphagous and other species of this group are oligophagous, the majority of species in this group are strict monophagous (species living only on one host-plant species) or non-strict monophagous (species living on few and related species).

Aphis (*A.*) *melosae* and *Aphis* (*A.*) sp. unpublished (Ortego 1998) are the only species of this group in South America living on Asteraceae (as well as *A. craccivora*). The apterous viviparous females of *Aphis* sp. are similar in size to the "big" specimens of *A.*(*A.*) *melosae,* but they do not have marginal papillae on abd.seg.II to VI. The "big" specimens can be differentiated from the apterous viviparous females of the other species of this group having marginal papillae on abd.seg.II to VI, *A.*(*A.*) *mulini* and *A.*(*A.*) *mulinicola,* for the following characters: (1) the ratio ant.VIpt/ant.VIb, more or less 1 in *mulinicola,* 1.5–1.8 in *mulini* and 1.7–2.4 in *melosae*; (2) the number of caudal hairs, 8–10 in *mulinicola,* 10–14 in *mulini* and 7–12 in *melosae*; and (3) the host-plant, *Mulinum* (Apiaceae) for *mulini* and *mulinicola* and *Grindelia* for *melosae.*

The "dwarf" apterous viviparous females of *A.*(*A.*) *melosae* can be differentiated from the other *Aphis* spp. of the nominotypical subgenus recorded in South America by the combination of its small size and the host-plant.

On the other hand, the metric characteristics of *A.*(*A.*) *melosae* and *A.*(*A.*) *marthae* Essig, 1953, which lives on *Quilaja saponaria* (Rosaceae) in Chile (Essig 1953, Remaudière 1994) are very close. *Aphis marthae* apterae and *A. melosae* "big" apterae are similar in size (BL). They can be differentiated by the general appearance; the front shape (deeply sinuate in *marthae,* and moderately sinuate in *melosae* "big"); the cauda shape (without constriction, nearly triangular in *marthae,* with constriction, fingerlike, in *melosae*); the marginal papillae on abd.seg.II–VI (papillae exceptionally present on *marthae* and exceptionally absent in *melosae* "big"); the secondary sensoria (always absent on *marthae* and commonly present in *melosae* "big"); the ratio u.r.s/h.t.II 0,91–1.16 in *marthae* and 1.11–1.32 in *melosae* "big"); and the ratio BL/rostrum (3.8–4.7 in *marthae* and 2.44–3.57 in *melosae* "big"). The alatae females of *A. marthae* have segmental bands on the abdomen and 11–21 secondary sensoria on ant.III; the alatae females of *A. melosae* have segmental bands only on abd.seg.VI-VIII and 7–13 secondary sensoria on ant.III.

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TWO NEOTROPICAL *HYPATOPA* WALSINGHAM (GELECHIOIDEA: COLEOPHORIDAE: BLASTOBASINAE) WITH RETRACTILE LABIAL PALPI: A PREVIOUSLY UNKNOWN LEPIDOPTERAN FEATURE

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Abstract.—***Hypatopa cryptopalpella,* n. sp.,** is described and *H. brevipalpella* Walsingham, 1897, is redescribed. Males of both species possess retractile labial palpi, a feature not known to occur elsewhere in Lepidoptera. Male sex scales on the distal segment of the labial palpi are associated with a deep invaginated pocket from the lower end of the frontoclypeus, extending within the head cavity to the area between the bases of the antennae. The invaginated pocket is filled with a copius brown mass that is believed to be a secretion deseminated by the male sex scales on the labial palpi. The location of the glandular cells cannot be identified until specimens suitable for histological sectioning become available. A lectotype is designated for *Auximobasis brevipalpella* Walsingham, 1897, and it is herein transferred to *Hypatopa* Walsingham, 1907 **(new combination).**

Key Words: retractile labial palpi, Blastobasini, Dominica, Grenada, West Indies

The Blastobasinae are small to medium-sized moths, with less than 150 species known world wide. This number, however, greatly underestimates the species richness of the group because many undescribed species, especially from North America and the Neotropics, are represented in museum collections. Although the blastobasine moths are probably one of the most commonly collected groups of Gelechioidea in the New World, this subfamily may be one least known to science.

Since Meyrick (1894) the Blastobasinae have been considered to be a monophyletic group. Recent studies (Adamski and Brown 1989; Hodges 1998) have corroborated this view and have rigorously established the monophyletic relationships among the genera and the phylogenetic relationships of the Blastobasinae within Gelechioidea. In this paper the Blastobasidae (*sensu* Adamski and Brown 1989) are treated as a subfamily within the Coleophoridae, following Hodges (1998), and *Hypatopa* Walsingham, 1907, to which the two species are assigned herein, are referred to the Blastobasini.

Nearly one-fourth of the 69 species of Neotropical Blastobasinae described are from the Lesser Antilles of the West Indies. All but one of these species, *Pigritia troctis* Meyrick, 1922, were described by Walsingham (1892, 1897), and most of these species are from St. Thomas. The remaining few species are from Grenada, St. Vincent, and Barbados.

Hypatopa includes 23 species from North American and several species from the Neotropics (new combinations of Walsingham, Meyrick, and Zeller to be recognized in the future by the author). More-

over, the genus contains dozens of undescribed species from both faunal regions known by the author.

This paper not only describes a new species of *Hypatopa* from Dominica but includes another previously described species and hypothesizes their relationship based upon the presence of retractile labial palpi, a feature not previously known to occur in Lepidoptera.

Methods

Adults were examined with an incandescent light source (reflected light). *The Methuen Handbook of Colour* (Kornerup and Wanscher 1978) was used as a color standard for the description of the adult. Genitalia were dissected as described by Clarke (1941), except mercurochrome and chlorazol black were used as stains. Slide preparations were examined with dissecting and compound microscopes. Measurements were made with a calibrated ocular micrometer. Names of genitalic structures are described and follow Adamski and Brown (1989).

The gross morphology of the head of *Hypatopa cryptopalpella* Adamski was studied after scales were removed using a fine camel's hair brush, cut about ⅛ length. Specimens were then placed in glycerine on a depression slide and illustrated using a camera-lucida.

The ultrastructure of the head of *Hypatopa cryptopalpella* was studied with an Hitachi HH-S-2R scanning electron microscope at an accelerating voltage of 20 kV. For SEM examination, heads and their appendages were obtained from pinned specimens, mounted on stubs with silver paint and paste, and coated with gold-palladium in a Polaron E5100 sputter coater.

Hypatopa cryptopalpella Adamski, new species

(Figs. 1–17, 20)

Diagnosis.—Male with retractile labial palpi, deep invaginated pocket from lower end of the frontoclypeus to the area between the bases of the antennal sockets; valva with dorsal articulation reflexed distally, forming an arch; sacculus smooth, except outer margin with a cluster of bladelike setae between a dorsal obtuse spine and a ventral row of long marginal setae; base of upper part of valva deeply dentate; apical process of lower part of valva reduced; anellus with two overlapping plates, each with marginal setae; antrum of female with two spinelike projections.

Description.—*Male head* (Figs. 2–3, 15): Vertex and frontoclypeus with grayish-brown scales tipped with pale grayish brown, or mostly with grayish-brown scales intermixed with pale-brown scales, or concolorous pale grayish-brown scales. One specimen near white, and few specimens with mostly orange-gray scales, intermixed with pale orange-gray scales; scales of vertex intermixed with few iridescent bluish-violet sex scales. Antennal scape and pedicel as above, except scape with iridescent bluish-violet squamiform sex scales on ventral surface and dorsodistal margins, and cylindrical sex scales on posterior margin near base (Figs. 12–14); squamiform sex scales of scape with narrow scutes and many windows (Fig. 14), as conpared to adjacent unspecialized scales with broad scutes and few windows (Fig. 15); flagellum grayish brown, with many short sensory hairs, nearly twice diameter of female flagellum; retractile labial palpus recurved in front of frontoclypeus (Figs. 5–6) or inserted into a deep invaginated pocket from lower end of frontoclypeus, extending within head cavity to the area between bases of antennal sockets (Figs. 2–3); labial palpus with basal segments pale grayish brown, terminal segment with elongate iridescent bluish-violet sex scales on apical part (Figs. 5–11); sex scales with scutes broad and spatulate, with a raised distal part, windows appear absent; proboscis patterned as frontoclypeus.

Female head (Fig. 4): As male, except sex scales and invaginated pocket absent; labial palpus longer than that of male (Fig.

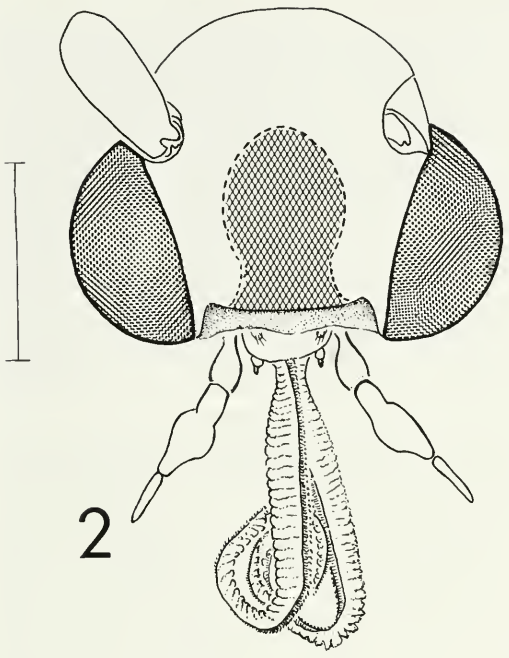
Fig. 1. Holotype of *Hypatopa cryptopalpella.*

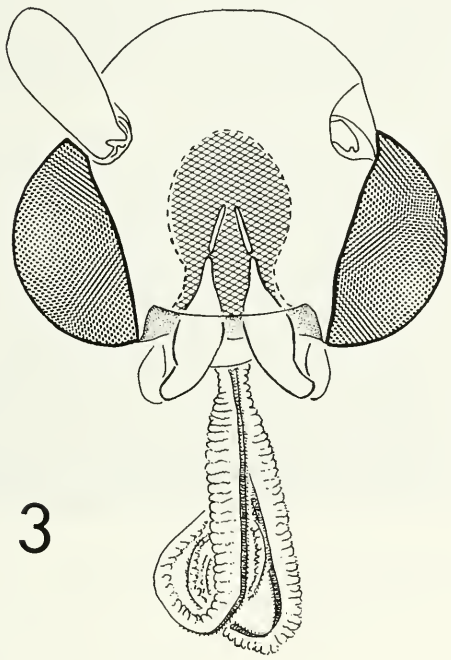
4), patterned as frontoclypeus, but paler on inner surface; second segment about twice length of terminal segment, basal segment short.

Thorax: Tegula and mesoscutum grayish brown intermixed with pale grayish-brown scales; male with dark brown-scales at base. Some specimens with tegula paler than mesoscutum. Legs with outer surface scales brown tipped with white, or brown intermixed with white scales; legs mostly white near distal end of segment and tarsomeres, forming ring pattern; inner surface mostly white, intermixed with few brown and pale-brown scales. Forewing (Fig. 1): length 4.9–6.0 mm (n = 33), mostly with pale orange-gray scales, or orange-gray scales tipped with white; male with some brown scales along base of costa and base of wing. Some specimens with distal ⅔ wing darker than basal ⅓. Discal cell with two brown spots near end of cell present or absent, midcell spot absent; undersurface uniform pale brown, except male with dark-brown scales at base extending to about ⅓ length of wing within cell; venation (Fig. 16) with four-branched cubitus; CuA_2 near right angle to base of M_2 and M_3. Hindwing pale brownish gray; venation (Fig. 17) with three-branched cubitus.

Abdomen: Pale grayish brown, except brown on ventrolateral surface.

Male genitalia (Fig. 17): Uncus absent; gnathos medially reduced beneath tuba analis; tergal setae present; vinculum a thin band; juxta divided; valva with dorsal articulation reflexed distally, forming an arch; sacculus smooth, except lower margin with a cluster of bladelike setae between a distal obtuse spine and a row of long proximo-





Figs. 2–3. Head of *Hypatopa cryptopalpella*. 2, Head with labial palpi extended. 3, Head with labial palpi within head capsule. Scale = 1.0 mm.

basal setae along margin; base of fingerlike upper part of valva with outer margin deeply dentate; apical process of lower part of valva reduced; aedeagus slightly angled, anellus with two overlapping plates, each with marginal setae.

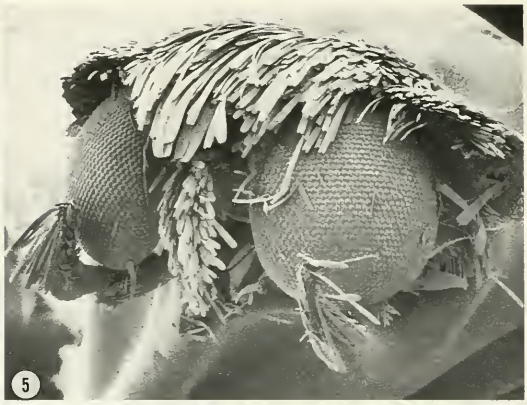
Female genitalia (Fig. 20): Ovipositor in four membranous telescopic subdivisions; ostium within membrane slightly posterior to segment seven; antrum membranous with two large spinelike projections, each pointed posteriorly, and convergent basally; inception of ductus seminalis within a slightly bulbous part of ductus bursae; corpus bursae subspherical, with spinelike signum.

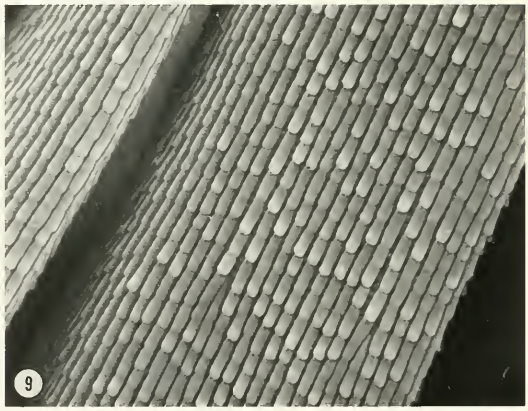
Holotype.—♂, "DOMINICA, Pont Casse, 2 mi[les] N[orth] W[est], V-1965, D. R. Davis". The holotype is not dissected and is deposited in the National Museum of Natural History [USNM], Smithsonian Institution, Washington, D.C., USA.

Paratypes.—12 ♂, 11 ♀, same data as holotype except, "♂ Genitalia Slide by DA 3471, USNM 81624" [green label]; "♂ Genitalia Slide by DA 3472, USNM 81625" [green label]; "♂ Wing Slide by DA 3475, USNM 81628" [green label]; "♀ Genitalia Slide by DA 3473, USNM 81626" [green label]; "♀ Genitalia Slide by DA 3474, USNM 81627" [green label]; "♀ Wing Slide by DA 3476, USNM 81629" [green label]. 3 ♂, 5 ♀, "DOMINICA B[ritish] W[est] I[ndies], Antrim 1000' [feet], 11-III-1956, J. F. G. Clarke", "Smithsonian Bredin Exped[ition]"; 5 ♂, 3 ♀, same data as above except, "18-III-1956"; 1 ♀, same data as above except, "10-III-1956"; 1 ♀, same data as above except, "22-III-1956". All paratypes are deposited in the National Museum of Natural History [USNM], Smithsonian Institution, Washington, D.C.

Etomology.—The Greek prefix *crypto* and the suffix, *palpella* together mean "hidden palpus", and refer to the retractile labial palpi of the male.

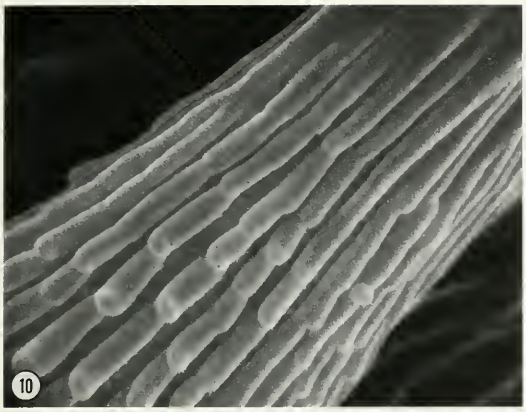
Remarks.—*Hypatopa cryptopalpella* differs from *H. brevipalpella* in having a gray-

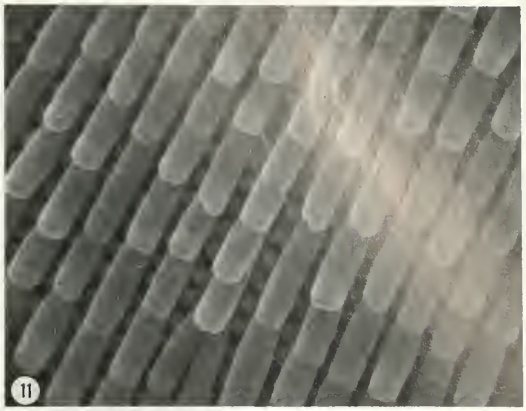


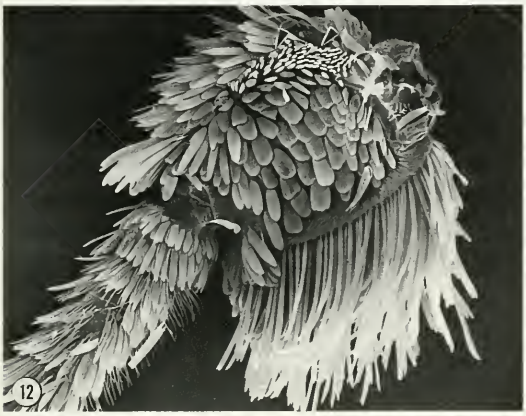


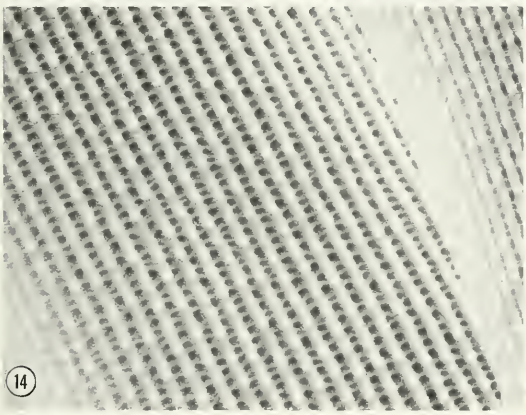
Figs. 4–9. Scanning electron micrographs of head of *Hypatopa cryptopalpella*. 4, Frontolateral view of female, 86×. 5, Frontolateral view of male, 102×. 6, Inner surface of male right labial palpus, 200×. 7, Lateral view of male right labial palpus, 250×. 8, Apical area of male right labial palpus, 650×. 9, Apical area of male sex scales on apical portion of labial palpus, 15,000×.

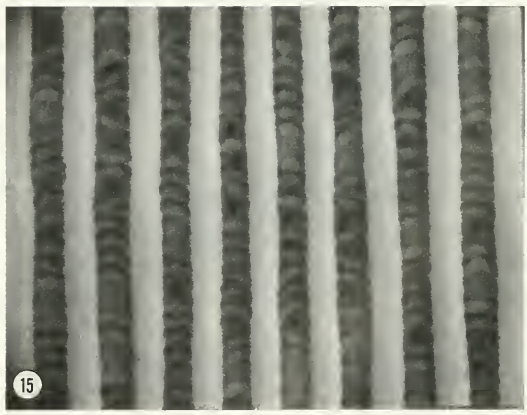
ish-orange or pale grayish-orange ground color of the forewings, midcell spot of the discal cell absent, and the median fascia absent. *H. brevipalpella* has a grayish-brown ground color of the forewings, all discal spots present, and an incomplete median fascia. Male and female genitalia of both species differ as figured.



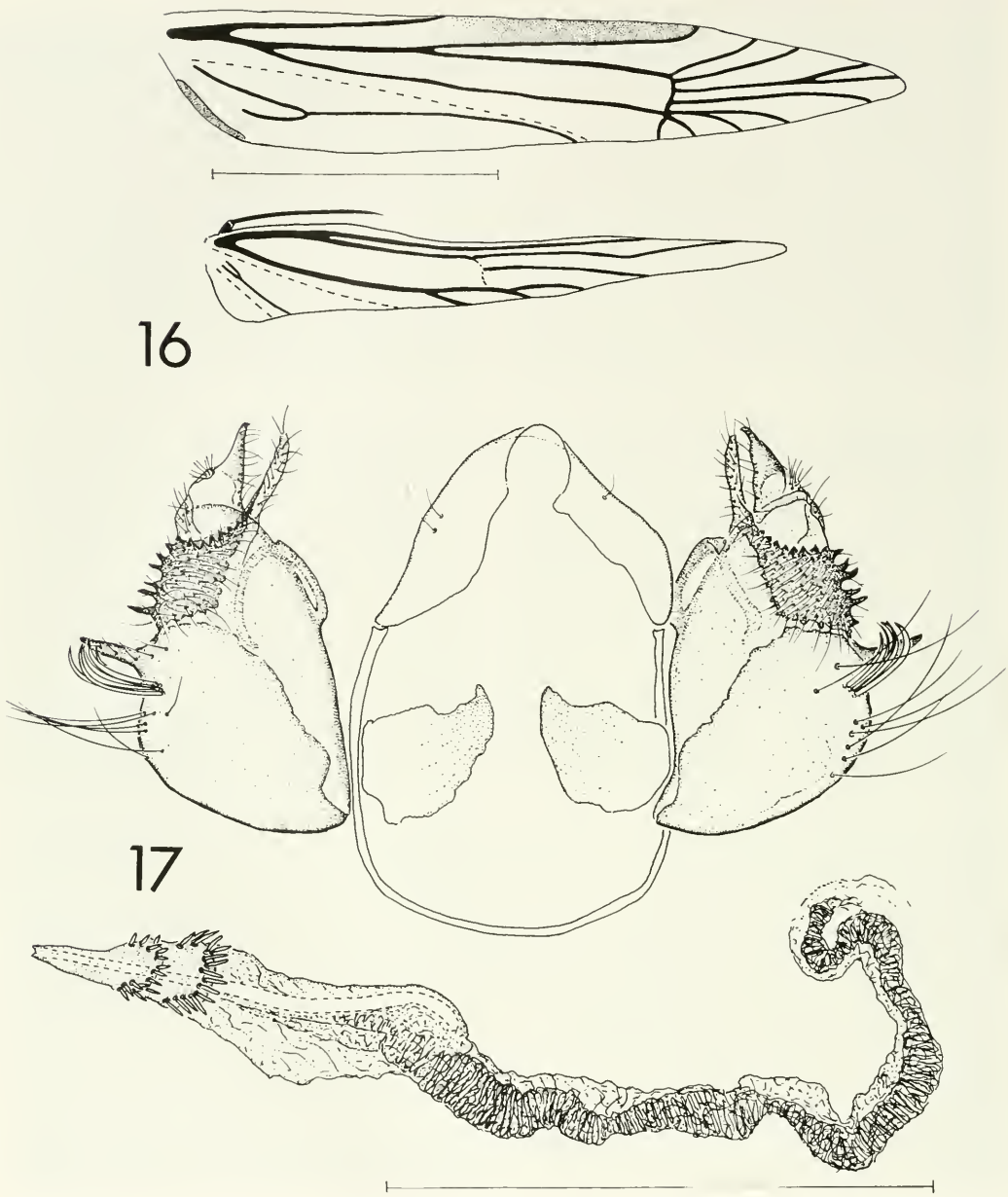








Figs. 10–15. Scanning electron micrographs of head scales of *Hypatopa cryptopalpella*. 10, Apical area of male sex scale on apical portion of labial palpus, 15,000×. 11, Central area of male sex scale on apical portion of labial palpus, 15,000×. 12, Undersurface of basal portion of male left antenna, note arrows pointing to cylindrical sex scales on posterior margin of scape, 175×. 13, Cylindrical sex scales on posterior margin of scape, 8,000×. 14, Squamiform scale on undersurface of male scape, 25,000×. 15, Squamiform unspecialized scale of scape, 7,750×.



Figs. 16–17 Wing venation and male genitalia of *Hypatopa cryptopalpella*. 16, Wing venation. Scale = 1.0 17, Male genital capsule and aedeagus. Scale = 0.5 mm.

Hypatopa brevipalpella (Walsingham 1897), **new combination**
(Figs. 18–19, 21)

Auximobasis brevipalpella Walsingham 1897:95; Becker 1984:41.

Diagnosis.—Male with retractile labial palpi, dorsal articulation of valva reflexed toward vinculum, sacculus setose, with a small cluster of stout setae near distal margin, juxta divided. Female with microtrichiate membrane surrounding ostium.

Fig. 18. Lactotype of Hypatopa brevipalpella.

Description.—*Head:* Vertex and frontoclypeus with scales mostly grayish brown, intermixed with grayish-brown scales tipped with pale grayish brown; distal portion of labial palpus inserted into a pocket in head capsule as in *H. cryptopalpella,* as far as could be ascertained without dissecting unique male specimen; visible basal portion grayish brown. Female labial palpus as in *H. cryptopalpella.* Antennal scape and pedicel as frontoclypeus, flagellum gray; proboscis pale brown.

Thorax: Tegula and mesoscutum mostly with brown scales, intermixed with brown scales tipped with pale brown, and pale-brown scales tipped with white. Legs with outer surfaces mostly brown, intermixed with pale-brown scales, and pale-brown scales tipped with white, inner surface mostly with pale-brown scales, intermixed with white scales. Scales mostly white near distal end of segments and tarsomeres. Forewing (Fig. 18): length 5.0–5.2 mm (n = 3), mostly grayish-brown scales, intermixed with pale grayish-brown scales and white scales; costal and outer margin brown, fringe scales between R_1 and R_5 with alternating pale and dark patches forming an irregular marginal pattern; median fascia incomplete, obliterated by pale-brown scales near midcell; two dark-brown spots near distal margin of cell, and one faint spot near midcell; a brown streak between wing base and median fascia, posterior to CuP. One specimen with distal ⅔ darker than basal ⅓. Undersurface brown. Hindwing pale brownish gray, gradually darkening to outer margin. Venation not studied.

Abdomen: Pale brownish gray.

Male genitalia (Fig. 19): Uncus short, apex rounded; gnathos forming a thin band around tuba analis; tergal setae present; vinculum, a thin ventral support; juxta divided; dorsal articulation of valva reflexed toward vinculum; distal process of lower division of valva not freely articulated with basal part; basal part with marginal setae; sacculus setose (with mostly hairlike setae), a small circular cluster of stout setae on distal part; distal process of upper division of valva with a sclerotized ridge fusing with sac-

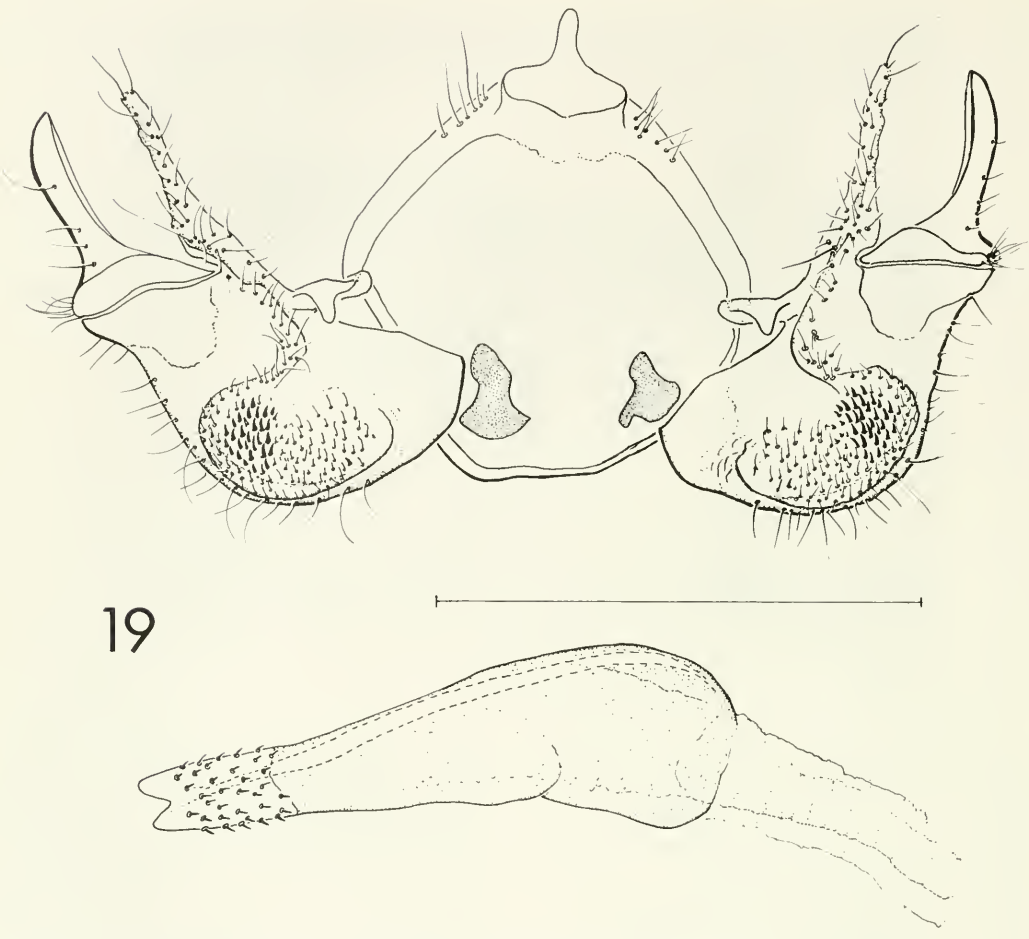


Fig. 19. Male genital capsule and aedeagus of *Hypatopa brevipalpella*. Scale = 0.5 mm.

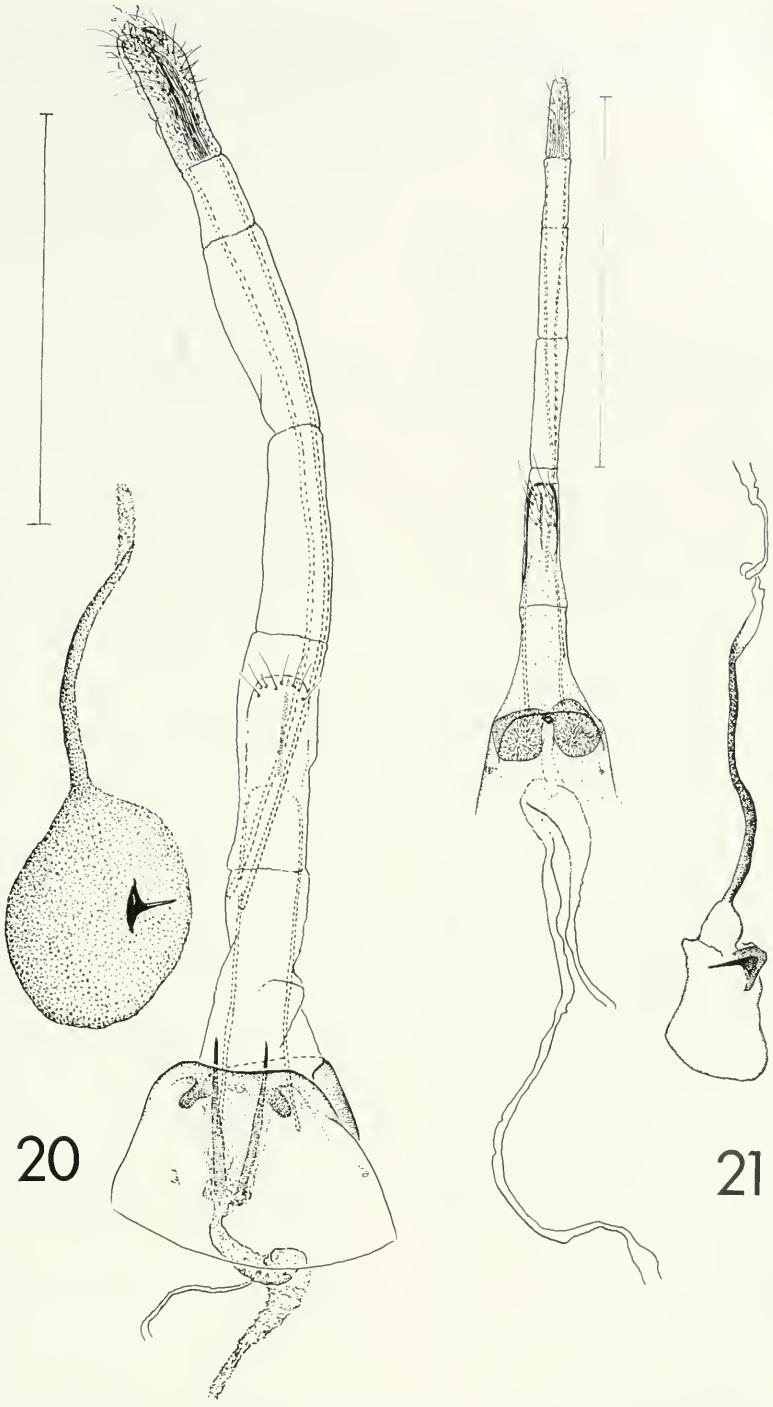
culus; upper part of valva setose. Aedeagus broad at base narrowing to apex; anellus uniformly setose.

Female genitalia (Fig. 21): Ovipositor as *H. cryptopalpella*; ostium within membrane slightly posterior to sternum seven; microtrichiate membrane surrounding ostium; inception of ductus bursae and ductus seminalis demarcated by short, parallel-sided membranous antrum; inner surface of anterior ⅓ of ductus bursae spinulate; corpus bursae with a spinelike signum.

Type examined.—Lectotype here designated, ♂, "Balthazar, Windward side, Grenada, W[est] I[ndies], H. H. Smith [Collector]". "BM-♂ genitalia slide no. 26567". In The Natural History Museum, London, England (BMNH).

Paralectotypes.—1 ♀, "Mount Gay, Est [action], (Leeward Side), Grenada, W[est] I[ndies], H. H. Smith, 25-30-VIII", "Walsingham Collection, 1910-427, 65298", "*Auximobasis brevipalpella* WLSM, Type ♀" [Specimen is missing abdomen]. 1 ♀, same data as above except, "Paratype ½", "BM ♀ genitalia slide no. BM 26568". 1 ♀, same data as above except, "I-5-X", "Walsingham Collection, 1910-427, 65305", "Paratype ½" [Specimen is not dissected]. All three paralectotypes are in BMNH.

Remarks.—Because only one male is



Figs. 20–21. Female genitalia of *Hypatopa* spp. 20, *H. cryptopalpella*. 21, *H. brevipalpella*. Scale = 1.0 mm.

known of this species, I did not dissect the head to confirm the presence of sex scales on the distal part of the labial palpi or the presence of the deep invaginated cranial pocket.

Discussion

The invaginated pocket found in male *H. cryptopalpella* is filled with a copius mass that is probably a secretion deseminated by sex scales on the labial palpi. The location of the glandular cells responsible for the secretion of this material cannot be identified until suitable specimens are available for histological studies.

The numerous genitalic differences between *Hypatopa cryptopalpella* and *H. brevipalpella* are hypothesized to be elaborations from different branches of the same evolutionary lineage. Consequently, the evolution of the retractile labial palpi in males and the deep invaginated cranial pocket are features that have evolved only once within this lineage. This hypothesis, however, can only be tested through phylogenetic analysis of *Hypatopa*.

Acknowledgments

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NATIVE BEES (HYMENOPTERA: APOIDEA) IN NATIVE TREES: *NYSSA SYLVATICA* MARSH. (CORNACEAE)

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Abstract.—*Nyssa sylvatica* (black gum, sour gum, pepperidge) is a functionally dioecious, insect-pollinated, ornamental, native tree that blooms from late May through early June in eastern Maryland. Its small, green flowers were visited for their abundant nectar and pollen by 46 species of native bees in 13 genera, and by other insects. Although honey bees were locally numerous, few (only 1.5% of all sampled bees), visited *N. sylvatica* and there was no evidence that they displaced native bees on this host. The inconspicuous flowers with vestigial green petals and sepals may attract pollinators by means of the lenslike, spherical droplets of nectar on glaucous floral discs that sparkle in the sunlight, and concentrate and reflect visible and ultraviolet light. Such flowers are here named "sparkle-flowers" (new coinage).

Key Words: *Nyssa,* Cornaceae, gum, tupelo, *Euphorbia, Hedera,* insect pollination, bees, competition, reflective nectar, ultraviolet, "sparkle-flowers"

The original vegetation of eastern North America after glaciation and before agriculture consisted of boreal, temperate and subtropical forests. The many native bee species of this region thus would be expected to be best adapted to forage primarily on native flowering forbs in spring before the forest canopy closes, and on the flowers of native trees and bushes. Our exotic agricultural crops, most ornamental plants, most weeds, and other plants that grow where the primeval forests have been cleared are visited by polylectic native bees, but these are not their original hosts. Surprisingly little is known about the bees and other insects that visit the flowers of our native North American trees, attention being diverted to the remote rainforests of Latin America. In order to learn about the normal relationships of native bees and their hosts, I observed and collected the insects visiting flowers of several species of native trees. Host trees surveyed included red maple, *Acer rubrum* L. (Batra 1985); Allegheny chinkapin, *Castanea pumila* (L.) Mill.; flowering dogwood, *Cornus florida* L.; sassafras, *Sassafras albidum* (Nutt.) Nees (Batra, unpublished), and black gum, *Nyssa sylvatica* Marsh. (this publication). The results of this basic research are expected to be useful for application in natural resource conservation, horticulture, plant breeding, wildlife management, and forestry.

The possible competition with native bees for floral resources by introduced European honey bees has recently become a controversial issue among conservationists (reviewed by Paton 1996). Therefore, *N. sylvatica* trees near a large apiary were included in the survey, to try to find out if honey bees had depleted nectar and pollen, and had displaced native bees.

Nyssa sylvatica is an abundant native tree

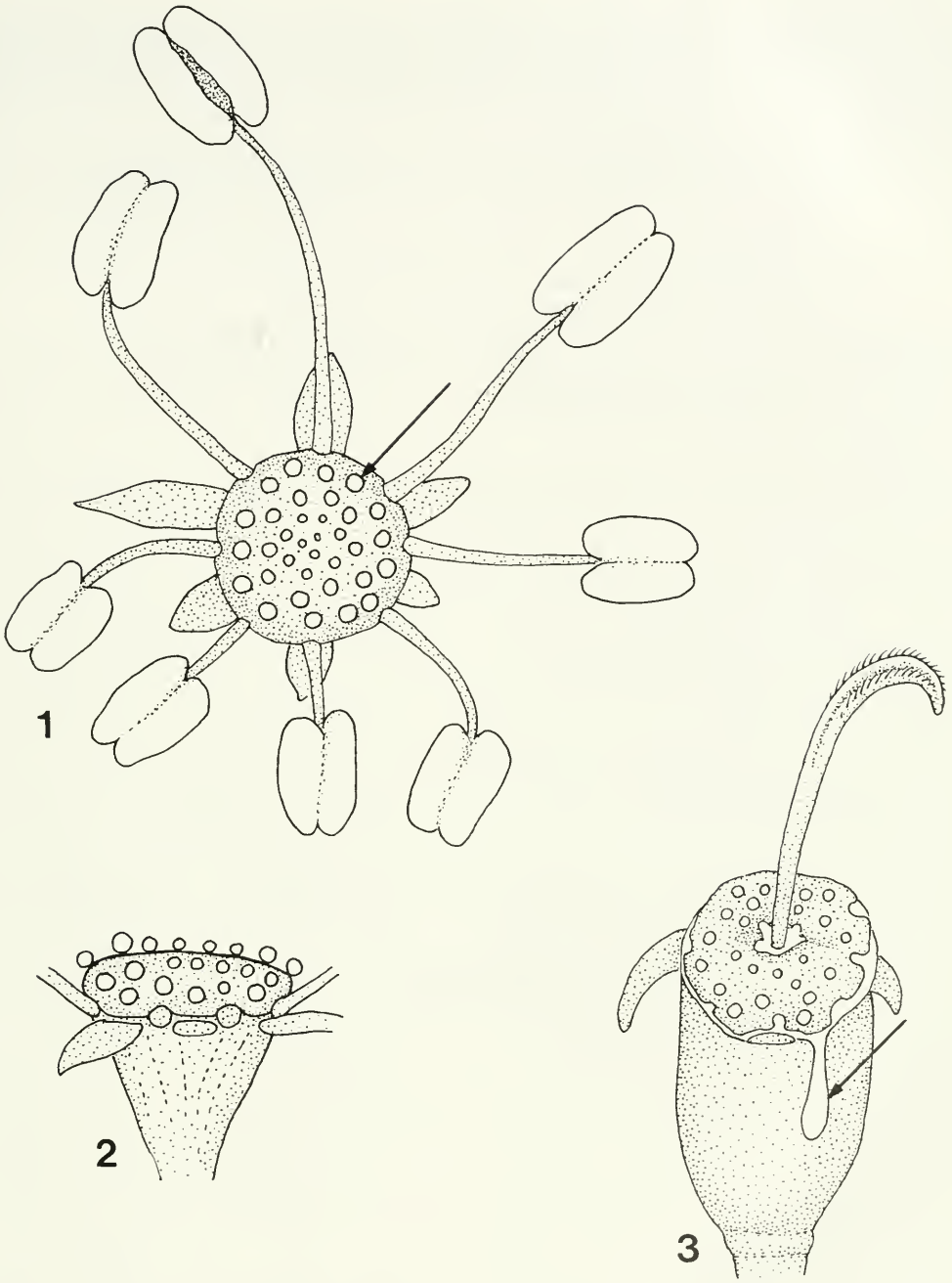
in the mesophytic forests of eastern North America. It ranges from southern Maine through southern Florida, and west through eastern Texas and Michigan, with a small population in the Mexican highlands (Eyde 1963, 1966). Popularly named black gum, black tupelo, sour gum, and pepperidge, it is cultivated as an ornamental tree because of the brilliant red and orange autumnal colors of its glossy leaves, and its attractively drooping, crooked branches. Birds eat its juicy, ovoid blue-black fruit (single-seeded drupes), disseminating this tree. The wood is used for veneer, containers, crossties and pallets.

There are seven species of *Nyssa* worldwide, five of them native to eastern North America, one in eastern China, and one in southeast Asia (Tandon and Herr 1971, Wen and Stuessy 1993). *Nyssa* is closely related to *Cornus,* and it has been included in the Nyssaceae (Eyde 1963, 1966; Tandon and Herr 1971; Cipollini and Stiles 1991) or the Cornaceae (Cronquist 1988). The tupelo, water gum, or white gum, (*N. aquatica* L.), grows in the swamps of the southeastern United States (Eyde 1963). Tupelo nectar is the source of a delicately flavored, expensive honey, which contains 48% levulose and 24% dextrose, and does not granulate; hives of honey bees are taken on barges into the swamps when tupelo blooms (Wood 1958, Rahmlow 1960a,b).

Staminate (male) and pistillate (female) flowers of *N. sylvatica* are borne on different trees; thus, this species is dioecious (Cipollini and Stiles 1991). A few pistillate flowers may have anthers with abortive pollen (Eyde 1963). Male trees bear more numerous and heavier flowers than do female trees. The depletion of nutrients caused by fruiting results in less frequent and less reliable flowering in female than in male trees (Cipollini and Stiles 1991). Flowers appear in the late spring, when the leaves are almost fully expanded. They grow on 3 to 6 cm long pedicels, often below the foliage and largely shaded by leaves. The small (ca. 8 mm long), green, inconspicuous pistillate flowers grow in groups of 2 to 4 on each pedicel. Clusters of staminate flowers are much more conspicuous, due to their larger size, their radiating yellow anthers on long filaments, and the glabrous discs of individual flowers. Several of the small, green staminate flowers (each 3 to 5 mm in diameter) grow on each pedicel, forming spheroid, umbel-like clusters of short racemes, up to 1.5 cm in diameter. Flowers of *N. sylvatica* would appear to be usually pollinated by the wind, due to their small size, green color, faint to no odor, and inconspicuousness. However, Eyde (1963) mentioned unspecified bees and other insects visiting them, also wind-borne pollen, collected 160 m from a tree. Three species of solitary bees, *Andrena hippotes* Robertson, *Perdita bradleyi* Viereck, and *P. townesi* Timberlake have been collected from flowers of *N. sylvatica* (Hurd 1979).

Flowering of *N. Sylvatica*

About twenty trees were studied from May 19 through June 9, 1997. They grew as scattered trees at the edge of a predominantly oak forest near the Bee Research Laboratory at Beltsville, MD, and in a suburban setting near my house in Greenbelt, MD, 4.8 km to the south. Insect visitors in the canopy were observed with the aid of 7 × 50 binoculars, and specimens on flowers were collected with a long-handled, aerial net. The weather was variable, being warm (to 36°C), dry, and sunny from May 19 through 23; cool and rainy from May 24 through 27; then mild and sunny from May 28 through June 9. Rain washed the exposed nectar from floral discs, but it was replenished during dry weather. Flowering began on May 22, when some anthers on the staminate flowers of male trees growing in sunny areas began to dehisce, and small, spherical droplets of nectar were simultaneously secreted (Figs. 1,2). Pistillate trees in sunny areas began to bloom on May 23, also secreting nectar, which accumulated at the bases of their erect green styles and in the grooves surrounding their floral discs



Figs. 1–3. "Sparkle-flowers" of *N. sylvatica*; the cushionlike floral discs are about 2 mm in diameter. 1, Young staminate flower with vestigial green petals, viewed from above; one stamen has elongated and its yellow anther has dehisced; the glaucous floral disc bears reflective droplets of nectar (arrow). 2, Lateral view of the disc of a staminate flower, showing how the spherical, lenslike droplets stand above its surface. 3, Young pistillate flower (oblique view), with droplets of nectar; some droplets have coalesced around the base of the style, and nectar oozes from the floral disc onto the ovary (arrow).

Table 1. Bees caught and seen on flowers of *N. sylvatica*. F = female or worker bee; M = male bee; P = bee is collecting pollen; G = at Greenbelt; B = at Beltsville. Some of the unidentified male and female *Andrena* may be of the same species (the sexes are dissimilar; there are many species of *Andrena*, and many are difficult to identify). The female *Andrena melanochroa* on pistillate flowers was carrying 50% *N. sylvatica* pollen in her well-filled scopae, this shows that bees can pollinate this tree and they will carry pollen a considerable distance (the nearest male tree was over 100 m away).

Bee species or genus, sex and number of individuals		On Male Trees	On Female Trees
Apidae			
2F	*Apis mellifera* L.	—	B
1F	*Bombus bimaculatus* Cresson	P, G	—
1F	*Bombus impatiens* Cresson	P, G	—
Anthophoridae			
1F, 1M	*Ceratina calcarata* Robertson	G	—
5F	*Nomada denticulata* Robertson	G, B	—
1F, 1M	*Xylocopa virginica* (L.)	G	
Megachilidae			
1F	*Chelostoma philadelphi* Robertson	—	G
2M	*Chelostoma philadelphi* Robertson	B	—
Halictidae			
5F	*Augochlora pura* (Say)	2 P, G, B	—
1F	*Dialictus cressoni* (Robertson)	B	—
1F	*D. rohweri* (Ellis)	G	—
1F	*D. tegularis* (Robertson)	B	—
2F	*D. versatus* (Robertson)	B	—
2F	*Dialictus* sp. 1	G, B	—
1F	*Halictus* (*Seladonia*) *confusus* Smith	B	—
5F	*Lasioglossum* sp. nr. *coriaceum* (Smith)	2 P, B	—
1F	*Lasioglossum* (*Evylaeus*) sp. 1	—	G
1F	*Sphecodes confertus* Say	G	—
Andrenidae			
15F	*Andrena* sp. nr. *confederata* Viereck	10 P, G, B	2, G
6M	*Andrena lamelliterga* Ribble	G, B	G, B
11F	*Andrena* sp. nr. *lata* Viereck	5 P, G, B	—
1F	*Andrena melanochroa* (Cockerell)	—	G
1M	*Andrena perplexa vibernella* Graenicher	B	—
2F	*Andrena perplexa vibernella* Graenicher	2 P, G	—
5F	*Andrena rugosa* Robertson	2 P, B	—
5F	*Andrena vicina* Smith	5 P, G, B	—
1M	*Andrena* (*Micrandrena*) sp.	—	G
2F	*Andrena* sp. 1	1 P, B	—
1F	*Andrena* sp. 2	—	B
5F	*Andrena* sp. 3	3 P, B, G	G
6F	*Andrena* sp. 4	3 P, B, G	G
2F	*Andrena* sp. 5	2 P, B	—
2F	*Andrena* sp. 6	1 P, B	—
1F	*Andrena* sp. 7	—	G
1F	*Andrena* sp. 8	B	—
3F	*Andrena* sp. 9	1 P, G, B	—
1F	*Andrena* sp. 10	G	—
1M	*Andrena* sp. 11	G	—
2M	*Andrena* sp. 12	—	G
5M	*Andrena* sp. 13	G	G, B
1M	*Andrena* sp. 14	G	—
1M	*Andrena* sp. 15	B	—
3M	*Andrena* sp. 16	—	G, B
1M	*Andrena* sp. 17	—	G

Table 1. Continued.

Bee species or genus, sex and number of individuals		On Male Trees	On Female Trees
Colletidae			
8 + F	*Colletes thoracicus* Smith	6 P, G, B	—
3 + M	*Colletes thoracicus* Smith	G, B	—
1F	*Colletes willistoni* Robertson	P, B	—
1F	*Hylaeus modestus* Say	B	—
3M	*Hylaeus modestus* Say	—	G

(Fig. 3). Flowering ended on June 9; the last trees to bloom being those growing in understory areas that were shaded by taller trees.

During warm, sunny weather, individual pistillate flowers began flowering (secreting nectar) and ceased flowering (stopped nectar secretion, with their styles curled, shriveled, and brownish) within 24 hours. For example, some pistillate flowers on one tree began secreting nectar and attracted insects at noon on May 23. They had presumably been fertilized by noon the next day, because they had ceased nectar production, and no longer were attracting insects. Other pistillate flowers on the same tree bloomed on other days, so that the total flowering period of this female tree lasted 10 days. The flowering period of individual staminate flowers lasted several days. During this time, nectar droplets were continuously secreted, and the numerous anthers on each flower dehisced sequentially (Fig. 1). Staminate trees collectively and individually had a long flowering period. At mid-bloom, each tree had some branches with flowers not yet blooming, other branches with flowers in full bloom, and some branches were past bloom, with shriveled stamens falling from their flowers.

Staminate flowers had a faint, pleasant, honeylike fragrance, but pistillate flowers seemed to me to be odorless. Both pistillate and staminate flowers produced copious nectar. When first secreted, the nectar appeared as small, discrete, transparent, shiny spheres on the glabrous floral discs (Fig. 2). These later enlarged (to 0.2–0.3 mm in diameter), then (at 0.5 mm) coalesced, to cover the disc with a sheet of glistening, dense, and sweet-tasting nectar. Excess nectar may drip from the discs of pistillate flowers (Fig. 3). Once the nectar has coalesced, the floral disc beneath it loses its pale, bluish glabrous appearance, and becomes dark green. Nectar secretion by staminate flowers begins as their first anthers dehisce (Fig. 1), and ends when all anthers have shriveled and some have begun to fall off.

In order to determine whether pollination by wind and insects occurs, several branches of a pistillate tree were securely bagged prior to bloom, and the bags were left in place for a month. Brown Kraft paper bags were used to exclude both wind-borne and insect-borne pollen. Fine-mesh gauze bags were used to exclude only insects. No fruit formed on any of the hundreds of bagged flowers, even though a few of them had vestigial anthers. This showed that cross pollination by insects is required.

Several other native woody plants in the area bloomed at the same time as *N. sylvatica*, potentially competing for visits by pollinating insects. These included huckleberry, *Gaylussacia frondosa* (L.) T. and G.; American holly, *Ilex opaca* Ait.; mountain laurel, *Kalmia latifolia* L.; tuliptree, *Liriodendron tulipfera* L.; staggerbush, *Lyonia mariana* (L.) D. Don; black cherry, *Prunus serotina* Ehrh.; black locust, *Robinia pseudoacacia* L.; poison ivy, *Rhus radicans* L.; *Rubus* sp. and *Viburnum* sp. Most of these plants had conspicuous, fragrant flowers. Many of the bees that were caught on *N. sylvatica* flowers included pollen of other plants in their scopae. Allegheny chinkapin, which is very attractive to many species of

bees and other insects, began to bloom a day after *N. sylvatica* finished blooming. American chestnut, *Castanea dentata* (Marsh.) Borkh., was once a dominant tree of the eastern mesophytic forest; its almost total loss must have significantly altered the numbers and diversity of insects that depended on its flowering.

Bees on *N. Sylvatica* Flowers

Bees and other insects were collected from the pistillate and staminate flowers of about 20 trees (Table 1). Binoculars were used to observe bees high in the canopy, where they could not be collected; these included numerous foraging females of *Colletes thoracicus* Smith, and both sexes of *Xylocopa virginica* (L.), including males patrolling and defending their territories. Both sexes of *C. thoracicus* were very abundant at mid-day on May 31 on a staminate tree in Greenbelt; some two females per cubic meter of canopy could be seen at a glance, while foraging for nectar and pollen. This bee is also often abundant on *Liriodendron tulipfera* and *Ilex* spp. trees. In general, more bees were seen on flowers of *N. sylvatica* that were in sunlight (in full sun or in sun flecks) than on those in shade (the shady side of the tree, or beneath taller trees, or shaded by the host's own canopy). During the course of a day, as individual *N. sylvatica* flowers became sunlit and shaded, bees usually visited them while they were in the sunshine.

Most of the bees on *N. sylvatica* flowers were short-tongued species in the genera *Andrena* and *Colletes*; over 135 individuals in 46 species, 13 genera, and 6 families were collected or seen (Table 1). Although bees predominated, other insects also visited *N. sylvatica* flowers (mostly staminate); they included thrips; syrphid, conopid, calliphorid, and other flies; *Polistes, Vespula* and solitary predaceous wasps; small parasitic wasps; carpenter ants; cantharid and cerambycid beetles; and adult sawflies.

Only two honey bees were collected or seen on flowers. They were on pistillate flowers within 50 meters of the apiary at Beltsville. At the time, this apiary had 73 large colonies with thousands of foragers in hives with 2 supers, plus 8 small colonies, or "nucs". Honey bees comprised only 3 percent of all bees collected from *N. sylvatica* flowers near the apiary at Beltsville (2 of 53), and only 1.5 percent of all bees collected (2 of 135). This result was surprising, because nectar was always abundant on pistillate and staminate flowers, and honey bees produce a large amount of honey for the commercial market from the nectar of tupelo trees (*N. aquatica*). However, *N. aquatica* and *N. sylvatica* may not be preferred hosts for honey bees. Perhaps they are forced to forage on tupelo due to the absence of other hosts in the southern swamps. Honey bees did not outcompete or displace native bees on *N. sylvatica* as expected, including trees growing near numerous hives.

The reasons for the attraction of bees and other insects to the small, green flowers of *N. sylvatica,* while more showy alternate hosts were available, were investigated. The staminate flowers have only a faint fragrance, and the radiating yellow anthers may be attractive (Fig. 1). Nectar exposed on the floral discs is readily accessible to many insects. However, if the easily ingested, noncrystallizing nectar sugars alone were the main attractant, *N. sylvatica* flowers would be expected to host a wide range of scavengers, and be teeming with these insects, as can be seen feeding on sap at slime fluxes. Instead, short-tongued bees predominated, accounting for about 70 percent of all insect visitors.

A remarkable feature of the flowers of *N. sylvatica* is the appearance of the exposed nectar when it is in sunlight. The small, spherical droplets on young flowers glitter against their background of pale blue-green, glaucous floral discs. The sheet of nectar on older flowers also glistens in the sunlight. Even slight movements of the branches cause the sunlit nectar to sparkle. The smooth, glossy upper surface of the leaves

also reflects sunlight, including ultraviolet (Fig. 7). It is probable that bees may be attracted at short range to the glittering of the nectar, which substitutes for the usual showy flowers with nectar guides and distinct fragrances, found among most insect-pollinated plants. Bees and flies are attracted to small, shiny objects of metal, and to glass beads (Peisl 1997); sparkling, colorless, odorless nectar may be similarly attractive. The shiny leaves of *N. sylvatica* may also serve to attract bees to the trees, acting as if floral clusters, by assisting in their long-range orientation. Most bee-pollinated flowers have distinctive shapes and colors that are attractive to bees, including patterns that reflect or absorb ultraviolet. They enhance bees' learning and memory, thus aiding floral constancy and pollen transmission (Menzel et al. 1997, Lehrer 1997). According to Chittka et al. (1994), green leaves appear uncolored to bees (=bee-white, bee-gray, bee-black), and most flowers have contrasting hues, including the surprisingly few (4%) that reflect only in UV, which is readily seen and remembered by bees. Most flowers contrast with surrounding foliage, which tends to absorb ultraviolet. The nectar and stamens of many flowers augment nectar-guide patterns on ultraviolet-reflecting petals, by absorbing ultraviolet light; they may fluoresce (Thorp et al. 1975, Tanaka 1982). The nectar droplets and opened anthers of *N. sylvatica* also fluoresce in ultraviolet.

The flowers of cypress spurge, *Euphorbia cyparissias* (L.), are also attractive to many bees and other insects (Batra, personal observation). They resemble flowers of *N. sylvatica* in visible light, because they are mostly green to greenish-yellow, and they also have exposed droplets of nectar in shallow nectaries. This nectar glistens in direct sun. I photographed flowers of *E. cyparissias* and *N. sylvatica* in sunlight, using a filter that transmits 350–390 nm ultraviolet wavelengths (Wratten 18A filter, Nikon 55 mm f/3.5 glass lens and Tri-X film). Foliage, bracts, and other parts of both plants that had appeared green to yellowish-green in daylight absorbed ultraviolet, appearing dark. The glistening nectar strongly reflected ultraviolet, appearing white, contrasting with the plants' flowers and foliage (Figs. 4–7). Evidently, insects are attracted by the nectar's reflected ultraviolet and visible light.

Thus, like *E. cyparissias,* the nectar of *N. sylvatica* reflects ultraviolet, contrasting with surrounding UV-absorbent green foliage, pedicels, and other floral structures. The reflectance may be enhanced in young flowers by the spherical shape of the discrete droplets, which would act as convex lenses, concentrating both visible and ultraviolet light. The bluish color of the background (the glabrous surface of the disc) may enhance the attractiveness of *N. sylvatica* nectar to bees, which respond to blue colors. Floral discs of young staminate flowers that bear numerous spherical, lens-like nectar droplets (Figs. 1,2) resemble the multifaceted lenses that are used as reflectors for traffic signals.

Honeydew that is secreted by aphids on conifers attracts bumble bees from long distances (Batra 1993). It also glitters brilliantly in the sunshine, contrasting with the dark green needles of the conifers. This may be another example of attraction by nectar-reflection; something worth reflecting about. Flowers that lack showy petals and sepals or a distinct perfume, and that rely on reflectance from their exposed nectar to attract pollinators, represent a distinct category or pollination system, here termed "sparkle-flowers" (new coinage). The small, yellowish-green flowers of ivy (*Hedera helix* L.) have exposed nectar droplets borne on convex discs (Barth 1985), thus resembling *Nyssa* flowers. They attract their host-specific pollinators (*Colletes hederae* Schmidt and Westrich) only when they are in sunshine (Westrich 1996). Thus, the flowers of ivy probably are yet another example of "sparkle flowers."

In conclusion, this preliminary research demonstrates that we should not assume

Figs. 4–7. Reflecting nectar of "sparkle-flowers," as seen in sunlight and in ultraviolet (as photographed with a Wratten 18A filter, Nikon 55 mm f/3.5 glass lens and Tri-X film). Reflective nectar droplets are indicated by arrows. 4, *Euphorbia cyparissias* in sunlight. 5, The same flowers in ultraviolet; white dots are UV-reflecting nectar droplets. 6, Staminate flowers of *N. sylvatica* in sunlight. 7, The same flowers in ultraviolet; note that the glossy tops of the leaves reflect.

that honey bees (or other exotic bees) compete with, and displace, native bees, even when honey bees are abundant, and a host that is known to be visited by honey bees is being considered. It will be necessary to study the complex of bee species that visit each host species during several seasons, to allow for annual fluctuations in weather, in native and exotic bee populations, in flowering of the host, and in the presence of other simultaneously flowering host plants that may divert bees (especially wide-ranging honey bees) from the plants that are being studied. Honey bees in this study evidently had been diverted from *N. sylvatica* to other, more attractive, resources.

The variety of bees collected from *N. sylvatica* during a short time, in a small area, suggests that more extensive surveys of this and other North American trees would yield many other insects, including undescribed species. Flowering trees often produce copious amounts of nectar and pollen, yet they are relatively unexamined resources that should have profound impacts on the population dynamics of our native bees. Beekeepers are aware of the value of several species of trees as resources for honey bees.

The discovery of "sparkle-flowers," a previously unrecognized type of inflorescence, in a suburban habitat that has been investigated by many scientists, shows that new phenomena can still be revealed in

such unpromising locations with the aid of simple, inexpensive equipment. The behavior of the bees as they approached flowers of *N. sylvatica* provided clues as to the attractant, much as did the behavior of insects at *Vaccinium* and *Gaylussacia* plants that had been infected by *Monilinia* fungi (Batra and Batra 1985). "Sparkle-flowers" may be a relatively common type of inflorescence, previously overlooked because they appear so inconspicuous to us.

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NOTE

Validation of *Neohydatothrips samayunkur* (Kudo) (Thysanoptera: Thripidae) for a Thrips Damaging Marigolds (*Tagetes* spp.)

Mound and Marullo (1996, Memoirs on Entomology International 6: 171) upon examining a paratype of *Neohydatothrips pseudoannulipes* Johansen (1983, Anales del Instituto de Biología Universidad Nacional Autónoma de Mexico 53: 108.) from Hidalgo, Mexico, concluded that the paratype and specimens collected on *Tagetes* sp. plants in Costa Rica were the same species and redescribed the species based on material from Costa Rica. Mound et al. (1996. Australian Journal of Entomology 35: 201) subsequently reported *N. pseudoannulipes* from Queensland and New South Wales, Australia, on *Tagetes erecta* L. and *T. minuta* L. Moreover, they treated *Hydatothrips* (*Neohydatothrips*) *samayunkur* Kudo (1995. Applied Entomology and Zoology 30:169) as a junior synonym of *N. pseudoannulipes*. Kudo described *H. samayunkur* from specimens collected on *Tagetes* sp. in Shizuoka, Japan, and also examined specimens from Okinawa and Hawaii where it was first reported as *N. variabilis* (Beach) (Tsuda and Sakimura. 1988. Proceedings of the Hawaiian Entomological Society 28:16).

After examining two paratypes of *N. pseudoannulipes* labeled with different collection data than the paratype examined by Mound and Marullo (1996) and specimens collected on marigolds from Hawaii and Australia, I conclude that the marigold specimens are not conspecific with *N. pseudoannulipes*. Therefore, *Hydatothrips samayunkur* Kudo is revalidated (**revised status**), and is further redesignated here as *Neohydatothrips samayunkur* (Kudo) (**new combination**). Moreover, *N. pseudoannulipes* is the correct name for the species described by Johansen (1983) and the description of *N. pseudoannulipes* in Mound and Marullo (1996) represents *N. samayunkur*. A non-type specimen from Mexico with the same collection date and locality as the paratype of *N. pseudoannulipes* examined by Mound and Marullo (1996) is identified here as *N. samayunkur*.

Neohydatothrips samayunkur and *N. pseudoannulipes* are similar in coloration of the antenna and body, but the brown bands on the forewings and the coloration of tibiae are different. *Neohydatothrips samayunkur* has the occipital apodeme on the head separated from the compound eyes, the forewing has a pale apical band and lacks setae on the hind vein, abdominal segment X is as brown as are segments VII–IX, and the tibiae are brown medially and otherwise yellow. In contrast, *N. pseudoannulipes* has the occipital apodeme touching the compound eyes, the forewing has a brown apical band and two setae on the hind vein within the brown band, abdominal segment X is pale, and the tibiae are completely yellow.

Neohydatothrips variabilis (Beach) is confused occasionally with *N. samayunkur* but is readily differentiated by the presence of two setae on the hind vein of the forewing, abdominal segments IX–X yellowish brown or paler than segments VII–VIII, and the hind tibiae completely yellow.

The current distribution of *N. samayunkur* is Costa Rica, El Salvador, Mexico (Hildago, Michoacán), United States (Florida, Hawaii), Australia (New South Wales, Queensland), Japan (Okinawa, Shizuoka), and Sri Lanka. Except for two countries, the reported hosts were marigolds (*Tagetes erecta* L., *T. minuta* L. and *Tagetes* sp.). Specimens from El Salvador were intercepted at agricultural quarantine, Houston,

TX, on unknown flowers. The slide label for a specimen from Hidalgo, Mexico, lists *Bidens, Eupatorium,* and *Salvia.* A specimen from Michoacán, Mexico was intercepted on grass at agricultural quarantine, San Ysidro, CA, in 1965.

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NOTE

Sialis vagans (Ross) (Megaloptera: Sialidae) and *Amphinemura nigritta* (Provancher) (Plecoptera: Nemouridae) Trapped by Mountain Laurel (*Kalmia latifolia* L.) (Ericaceae) Flowers

While sampling a small impoundment in the Frederick City Municipal Forest along Little Fishing Creek (Frederick Co., Maryland) on May 24, 1998, we observed mountain laurel (*Kalmia latifolia* L.) in full bloom around the pond. Closer examination of the floral clusters revealed large numbers of adult alderflies (Megaloptera: Sialidae). Some alderflies appeared to be stuck to the stems of the flowers by their tarsi; others were stuck to the corolla of the flowers by their wings. Although some of the specimens were dead, many were alive. As we removed several alderflies, we noted that the stalk, calyx, and corolla of the flowers were sticky to the touch.

We determined the number of floral clusters on two bushes (approximately 1.3 m in height) within 1–2 meters of the pond margin, and on a third bush along Little Fishing Creek exiting the pond. The two bushes along the margin of the pond had 25 and 97 floral clusters; the one along the stream had 18. We also counted the adult alderflies on each bush. Those along the pond margin contained 22 and 27 adult alderflies. Similar numbers of alderflies were found on other bushes along the pond margin. The bush along the stream had not trapped any alderflies; however, we did recover 10 stoneflies (Plecoptera) from the floral clusters. Dr. Oliver S. Flint, Jr. (Department of Entomology, Smithsonian Institution, Washington, D.C.) identified the alderflies as *Sialis vagans* (Ross) (Megaloptera: Sialidae). Ross (Ross. 1937. Bulletin of the Illinois National History Survey 21(3): 57–78) first described this species from specimens collected from lakes and rivers. Dr. Charles Nelson (Department of Biological and Environmental Sciences, University of Tennessee at Chattanooga, Chattanooga, TN) determined the stoneflies to be *Amphinemura nigritta* (Provancher) (Plecoptera: Nemouridae).

Mountain laurel is a common shrub distributed from Maine to Mississippi and Alabama. The inflorescence consists of terminal convex flower clusters. Richard A. Jaynes (Jaynes, 1997. *Kalmia:* Mountain Laurel and Related Species, Timber Press) indicates that the stalk, calyx, and corolla of *K. latifolia* flowers are covered with glandular, sticky hairs. This sticky secretion is believed to prevent access of crawling insects to pollen and nectar.

The poisonous properties of mountain laurel sap are well documented (Jaynes, 1988. *Kalmia:* The Laurel Book II, Timber Press). The sap contains a group of related

grayanotoxins (Mancini and Edwards. 1979. Journal of Natural Products 42(5): 483–488), which occur in a number of species of *Kalmia* and other genera in the Ericaceae. Nonetheless, it is not clear whether the alderflies and stoneflies stuck to the flowers actually died of poisoning or desiccation.

How both insect species moved to the mountain laurel flowers is not known. *Sialis vagans* and *A. nigritta* in flight may have selected the mountain laurel bushes along the pond and stream margins to rest or mate. They may also have emerged at or near the pond and stream margins, crawled up the bushes to expand their wings, and become stuck to the flowers as they climbed.

This novel observation may prove useful to collectors, as more taxa may be collected from mountain laurel flowers.

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NOTE

New Synonymies in Australia *Psix* Kozlov and Lê (Hymenoptera: Scelionidae: Telenominae)

Johnson and Masner (1985. Systematic Entomology 10: 33–58) revised the world species of the telenomine genus *Psix* Kozlov and Lê, recognizing 18 species. The genus is primarily found in the Old World tropics, with at least one probable accidental introduction into the New World. In fact, several species had been described before Kozlov and Lê (1976. Zoologicheskii Zhurnal 55: 143–145) first described the genus from Afghanistan. The varied placement of these early species reflected the confused taxonomy surrounding the large genera *Telenomus* Haliday and *Trissolcus* Ashmead. The work of Nixon (1935. Transactions of the Royal Entomological Society of London 83: 73–103, and subsequent papers) allowed us to recognize species of *Psix* among the Afrotropical and Oriental *Trissolcus* (then known as *Microphanurus* Kieffer). However, the Australian species were a more difficult problem. Dodd, beginning in 1913, described 102 species of Telenominae, but because he had to rely solely upon the vague, insufficient, and sometimes inaccurate descriptions available at the time, it was difficult to equate his generic concepts with those that developed and were accepted in later years. Johnson and Masner (1985) were able to recognize that *Telenomus olympus* Dodd was, in fact, a species of *Psix* on the basis of a specimen identified by Dodd in the Australian National Insect Collection. Correct generic assignment of the bulk of his species, however, required first-hand examination of the remaining type material.

Johnson (1988. Proceedings of the Entomological Society of Washington 90: 229–243) reported on the types of Australian species of telenomines described by Dodd and recognized that two further spe-

cies should be placed in the genus *Psix: Telenomus elpenor* Dodd and *Telenomus omphale* Dodd. However, the relationship of these two taxa to the species recognized in Johnson and Masner (1985) was not resolved. Through the kindness of Dr. Gordon Gross of the South Australian Museum, I have been able to study the unique specimens of these two Australian *Psix* and place them in their proper context.

Psix elpenor (Dodd) was described from two female specimens collected in Kuranda, northern Queensland (16°40′S, 145°38′E). Dodd's description is based entirely on a comparison with the species *Psix olympus* (Dodd), the primary distinguishing characteristic being the difference in size between the two (*P. elpenor* "much larger"). I believe these specimens belong to the same species, with the name *Telenomus elpenor* Dodd, 1914 becoming a junior synonym of *Telenomus olympus* Dodd, 1913 (**new synonymy**). *Psix olympus* is characterized by the acutely tridentate mandibles, the light-colored radicle, and the absence of notauli. The species is known only from the forests of eastern Queensland, from Mt. Tamborine in the south, north to Mossman.

Psix omphale (Dodd) was described from a single female specimen collected in Nelson (present day Gordonvale), Queensland (17°05′S, 145°47′E). I earlier reported (Johnson 1988) that the radicles of the antennae are missing from the holotype. They are absent from the slide mount of the antennae, but in fact are still attached to the head of the point-mounted specimen, hidden in the glue that covers the lower part of the face and mouthparts. Most *Psix* species are noteworthy for the contrast in color between the radicle (dark brown to black) and the remainder of the scape (usually yellow), a characteristic quite useful in separating some Australian species. The radicle of *P. omphale* is dark, and this specimen belongs to the complex of three closely related species, *P. fusus* Johnson and Masner, *P. metopa* Johnson and Masner, and *P. glabriscrobus* (Girault). The fore and mid coxae are clearly separated by the mesepisterna, thus eliminating *P. fusus*. The specimen is very similar to *P. glabriscrobus*, except for the near absence of any transverse microsculpture on the second metasomatic tergite. Its body shape, however, matches the stout form of *P. glabriscrobus* and not the more elongate habitus of *P. metopa*. Thus, I conclude that *Telenomus omphale* Dodd, 1913, and *Telenomus glabriscrobus* Girault, 1916, are synonyms, with Dodd's name now replacing that of Girault as the valid name for the species (**new synonymy**). *Psix omphale* appears to be widely distributed through eastern and central Australia.

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Book Review

Revision der "Lestremiinae" (Diptera, Cecidomyiidae) der Holarktis. Mathias Jaschhof. Studia Dipterologia—Supplement 4. Ampyx-Verlag 1998. 552 pp. Softbound. ISBN 3-932795-03-2. E-mail: ampyxstark@aol.com.

Lestremiinae are the oldest subfamily of Cecidomyiidae, more comparable in their fungal diet, distribution, and presumed age to Mycetophilidae than to the more derived, plant-feeding members of their own family. While the subfamily lacks the direct economic importance of its plant-feeding cousins, it is nonetheless fascinating for its great diversity and for being the source of the rest of the family.

The cover's design of a remarkable assortment of 24 lestremiine gonostyli and a cladogram is a winning introduction to the book, showing at the same time some of the groups's diversity and the establishment of order out of chaos. This study, the result of a thesis for the PhD at the University of Greifswald, Germany, is the first Holarctic revision of the subfamily. The Nearctic species were last revised in their entirety by A. E. Pritchard between 1947 to 1951. Since then, only a few papers have been published on the North American fauna, chiefly in response to need, most notably the revision of *Anarete* by K. C. Kim in 1967 in support of ecological studies by H. C. Chiang on swarming behavior. In the Palearctic Region, however, the study of this group has attracted a number of specialists, notably B. M. Mamaev, working from 1960 to the present mainly on adult taxonomy but also with larval biology. The Palearctic fauna was in particular need of revision because of the large number of available names and the piecemeal method of its investigation to date.

In this work the 528 known species names in Lestremiinae are reduced to 318 valid species. Of the latter number, only 92 are Nearctic, reflecting the limited attention this subfamily has received in North America, and 52 species are Holarctic in distribution. *Anarete* and *Conarete* are treated only as generic entities without species revision. These two genera are poorly represented in Europe and the revisions by Kim and Pritchard, respectively, can still serve. Three monotypic genera, *Groveriella, Yukawamyia,* and *Baeonotus,* are not treated because Jaschhof did not see specimens.

Jaschhof presents a fine modern revision. The book includes: overviews of adult Lestremiinae; analyses of zoogeography and the place of the subfamily within the family and order; a fine section on adult morphology; a historical review of taxonomic work; and a summary of methods of collection and study. The book has also a key to tribes and genera and, for some large genera, subgenera and species groups. Keys to species follow the separate generic treatments. There is no mention of larvae. This lack is forgivable in that larvae are known for few species and not all genera and their inclusion would have been too much to manage in the time available.

The descriptions for the adult stage of genera and species are thorough, the methodology careful and consistent throughout, and the illustrations superb. Figures for each species include, as available, details of the gonostylus (often shown in different aspects), tegmen, penis, and ninth tergite, the fourth flagellomere, and the palpus, and occasionally the spermathecae, variation in the genital apodeme, the head, the female postabdomen, and parts of the wing. Descriptions of the 55 species recently described by Jaschhof elsewhere are not repeated here to save space and cost, but illustrations for these species do appear here as well as discussions of relationships for each.

Results of the author's methodical anal-

ysis of 41 characters are summarized effectively in two cladograms. The author found that the many character regressions and convergences made it difficult to interpret with confidence some of the supraspecific groups. The Lestremiinae are paraphyletic to the monophyletic remainder of the Cecidomyiidae, and the source of the latter appears to be among the tribe Catochini. Jaschhof is careful to treat his classification as tentative, holding out the hope that further collecting and the study of larvae and extraterritorial lestremiines will make possible a thoroughly monophyletic classification.

Other than one junior generic synonym and two junior specific synonyms unaccountably missing, I found only a few slight errors. A single index to species and genera would have been easier to use than the separate species and generic indices given here, and it would have been helpful to give page references for junior synonyms instead of only referring them to their senior synonyms.

The book is printed on glossy paper with excellent reproduction of the author's fine drawings. As the reader will have noticed from the title, the book is in German, but included are an English summary and an English glossary/synopsis of the morphological terminology used. This latter feature should allow a non German-reader the use of the keys and appreciation of the cladograms. The figures are, of course, each worth a thousand words in any language.

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Reports of Officers

Editor

Volume 100 of the *Proceedings* totaled 844 pages. Eighty articles, 5 notes, 1 book review, 1 obituary, and the minutes of Society meetings were published.

Two *Memoirs* were published, *Memoir* 20 "The Genera of Elaphidiini Thomson 1864 (Coleoptera: Cerambycidae)" by Steven W. Lingafelter, and *Memoir* 21 "New World *Blepharida* Chevrolat 1836 (Coleoptera: Chrysomelidae: Alticinae)" by David G. Furth. Memoir 22, "Systematics of the North America species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae)" by John D. Pinto, is at the press and will be out at the end of the year on the first of 1999.

I extend my appreciation to Gary Miller for his continuing efforts to acquire informative book reviews, and to Tom Henry and Wayne Mathis, members of the Publications Committee, for their continued advice and support. I thank Marie Blair and Cathy Anderson for their much needed assistance in handling correspondence, routing manuscripts, and preparation of manuscripts and plates for the printer. Without their help, my job would have been much more difficult.

I am also grateful to the many reviewers for the time-consuming efforts and constructive reviews. Their contributions are essential to help increase the quality of papers published in the *Proceedings*.

Respectfully submitted,
David R. Smith, *Editor*

Treasurer

Summary Financial Statement for 1998

	General Fund	Special Publications Fund	Total Assets
Assets: November 1, 1997	$14,836.30	$107,833.41	$122,669.71
Total Receipts for 1998	62,637.11	17,210.80	79,847.91
Total Disbursements for 1998	66,842.67–	13,973.30–	80,815.97
Assets: October 31, 1998	10,630.74	111,070.91	121,701.65
Net Changes in Funds	$ (4,205.56)	$ 3,237.50	$ (986.06)

Audited by the Auditing Committee, January 11, 1999, consisting of Donald M. Anderson, Steven W. Lingafelter, and Norman E. Woodley, Chair. Presented to the membership at the meeting of December 3, 1998.

Respectfully submitted,
Michael G. Pogue, *Treasurer*

Membership

In 1998 the Society received applications for new membership from 19 people as follows:

Tevis Baier
Douglas C. Currie
Bonny Dodson
David A. Etnier
George A. Foster
Volker Hollman-Schirrmacher
Nayeem Hoq
Matthew D. Kane
Louis M. LaPierre
Jeng Ming-Luen
Bradley A. Mullens
Ronald Ochoa
J. H. Pedrosa-Macedo
J. Marc Revol
Leopold M. Rueda
Vera Cristina Silva
John Swann
Stephen J. Taft
John Wilterding

Each applicant was sent a letter acknowledging receipt of his/her application, and his/her name was read at a regular meeting of the Society and repeated in the minutes of the following meeting. The number of applications for new membership showed a slight decrease from 1997.

Respectfully submitted,
John W. Brown
Membership Chair

PROC. ENTOMOL. SOC. WASH.
101(2), 1999, p. 465

New Society Publications

(see inside back cover for ordering information)

New World *Blepharida* Chevrolat 1836 (Coleoptera: Chrysomelidae: Alticinae)
by David G. Furth
Memoir No. 21, 109 pp., 1998

Thirty-eight New World species of leaf beetles are treated. A key is provided and each species is illustrated.

Systematics of the North American Species of *Trichogramma* Westood
(Hymenoptera: Trichogrammatidae)
by John D. Pinto
Memoir No. 22, 287 pp., 1999

This is the first revision of this beneficial group which is important in biological control. A total of 68 species are included, with a key, distribution maps, and illustrations. The scope includes all of North America, including Central America.

PROC. ENTOMOL. SOC. WASH.
101(2), 1999, pp. 466–468

Society Meetings

1,032nd Regular Meeting—October 1, 1998

The 1,032nd regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:39 pm by President Warren Steiner, in the Waldo Schmitt Room of the National Museum of Natural History, Washington, D.C. In the absence of a gavel, President Steiner used an electric plug to bring the angry mob to order. Fourteen members and 8 guests were present. Minutes of the 1,029th and 1,030th meetings were read by pinch-hitting secretary John Brown, and were accepted with minor modification.

President Steiner's request for reports from the committees was answered by Brown, Membership Chair, who read the names of 11 new applicants for membership: Louis LaPierre, J. Marc Revol, David Etnier, Leopold Rueda, Bonny Dodson, Douglas Currie, John Swann, Vera Cristina Silva, Matthew Kane, Tevis Baier, and George Foster. One new member was present—George Foster. Guests in attendance were introduced.

President Steiner announced that time was approaching to compile a slate of candidates for Society officers for next year. He solicited volunteers either to be on the nominating committee or to serve as officers, and asked for nominations for honorary membership.

In Furth's absence the show-and-tell portion of the program was brief. Ralph Eckerlin presented a few comments on a recent meeting of the Washington Academy of Sciences, at which he represented ESW; and Jil Swearinger shared with the group her lovely new dung beetle earrings.

President Steiner introduced the evening's speaker, Dr. Charles Triplehorn of Ohio State University, whose football team currently is ranked number 1 in the nation. Dr. Triplehorn's talk, entitled "The rest of the story: a darkling beetle chronicle," was an interesting and entertaining look at the joyful field work, interesting personal associations, and gorgeous scenery "behind the scenes" of most of the mundane, though useful, taxonomic works that so many of us produce. The talk was illustrated by title pages of publications, photographs and drawings of tenebrionid beetles, and scenic natural landscapes. Triplehorn's astute summation of the fact that when you're sick and tired of a paper, its probably done, struck a responsive chord with many of those present.

The meeting was adjourned at 8:40 pm. Refreshments were provided by Jil Swearingen.

Respectfully submitted,
John W. Brown,
acting Recording Secretary

1,033rd Regular Meeting—November 5, 1998

The 1,033rd regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:30 pm by President Warren Steiner, in the Waldo Schmidt Room of the National Museum of Natural History, Washington, D.C. Sixteen members and eleven guests attended. John Brown's minutes from the 1,032nd Regular Meeting were read and approved with minor modification.

President Steiner asked for reports from the committees. John Brown, Membership Chair, read the names of two new members in ESW: John Wilterding, a graduate student at Michigan State University, and Dr. J. H. Pedrosa-Macedo, at the Labortorio de Proteção Florestal, Curitiba, Brazil.

Chris Thompson listed the ESW officer candidates for next year, noting that, with few exceptions, officers from this year offerred to continue in their positions. As always, additional candidates can be taken from the floor before the vote.

Ed Barrows presented a collection of sawflies taken in a survey of Malaise traps

suspended high over water. Gabriela Chavarría displayed the handsome T-shirts still available from the Pollinator Conservation event last June, noting that all profits from T-shirt sales will fund on-the-ground conservation projects. Ralph Eckerlin displayed a collection of staphylinids found on Central American mice; whether the beetles are parasitic or phoretic is unknown. Ed Saugstad passed around a 1/2 Penny token from 1793 featuring an image of a bee hive.

David Furth introduced Dr. Martha Weiss, an ecological entomologist at Georgetown University. She quickly set the tone of the evening by paraphrasing her presentation's scholarly title "Defecation Ecology: Why do Silver-Spotted Skippers Eject Their Frass?" as "Why do the caterpillars shoot their poop?" The silver-spotted skipper is a legume specialist that, as a caterpillar, builds shelters and ejects its frass, building different kinds of shelters as it grows. She described the amazingly regular ontogenetic sequence of shelter-type and proposed mechanisms by which the larvae achieve an accuracy of 0.1 mm in leaf-cut distances. Dr. Weiss also described likely mechanisms of how caterpillars shoot their poop, which appears to be from changing homeostatic pressure rather than a simple flick. She generously revealed to the audience her unpublished datum of the world's record holder for frass ejection distance, which is not included in these minutes so as to avoid scooping her poop shooter news. Her lab is currently exploring three evolutionary hypotheses of why the silver-spotted skipper shoots its poop: predator/parasitoid evasion; hygiene; and space conservation. She closed by asking the audience about frass ejection in their own organisms—their study organisms, that is.

The meeting was implicitly adjourned around 8:30 pm as the rowdy crowd broke up.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,034th Regular Meeting—December 3, 1998

The 1,034th regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:35 pm by President Warren Steiner, in the Waldo Schmidt Room of the National Museum of Natural History, Washington, D.C. Twenty members and twenty seven guests attended. The minutes from the 1,033rd Regular Meeting were read and approved with minor modification.

President Steiner asked for reports from the committees. John Brown, Membership Chair, reported that there were no new members in ESW, and none was present at the meeting. Fourteen guests from the USA, Russia, Spain, and Germany were introduced.

President Steiner thanked the ESW officers, past president, and president-elect, for helping make a good year of Society activities. Dave Smith (Editor) read his annual report. The Treasurer's annual report and the proposed amendments to the bylaws were passed around the room. Our accounts dropped by over $1,000 but we are still in the black. The ESW gained 19 new members during the year.

Chris Thompson listed the new ESW officer candidates for next year: President, Mike Schauff; Recording Secretary, Stu McKamey; Corresponding Secretary, Holly Williams; Custodian, Andy Jensen; Treasurer, Mike Pogue; Program Chair, John Brown; Membership Chair, Steve Lingafelter; Editor, Dave Smith; and President-elect, Dave Adamski and Dave Furth (a new candidate nominated from the floor). At Chris Thompson's suggestion, the uncontested seats were unanimously accepted. A written ballot was made for president-elect, with Furth winning the position.

The proposed amendments to the ESW bylaws were discussed: that the Program Chair serve a "Program Year" rather than a calendar year (Art. V.13, from Dave Furth); that the number of honorary mem-

bers be increased from 3 to 6 (and from 4 to 7, if one of the members is elected as honorary president) (Art. III.7, from Steiner); and that the recommended order of business be changed such that visitors be introduced after new members are introduced (Art. VIII.2–3, from Steiner). The vote will be taken at the next meeting if a quorum is present.

For exhibits, Ed Barrows (Georgetown University) showed slides of Dyke Marsh, Va., where he is conducting an insect survey, including floating Malaise traps. Dave Furth showed two beetle T-shirts available; Terry Lachman countered with a T-shirt from John May Museum of Boulder, Colo., covered with exquisitely realistic illustrations of many insects. Stu McKamey announced the upcoming new on-line resource "New Entomological Taxa," and Chris Thompson correctly pointed out that they have not yet announced the subscription rates. Alma Solis announced that she will be gone all of calendar year 1999.

Dave Furth introduced the evening's speaker, David L. Wagner, from the University of Connecticut. The title of his presentation was "Natural History and Defense Strategies of Caterpillars." Dr. Wagner began his talk with a synopsis of mortality factors of immature Lepidoptera. He then focused in on the importance of avian predators, arguing that birds affect not only what a caterpillar looks like, but also how it eats, when it eats, and even, perhaps, what it eats. Using images from his recently published caterpillar book, Wagner reviewed many of the strategies that palatable caterpillars use to avoid or deceive birds, from the obvious background matching to those that appear to resemble bird poop, plant debris, snakes, and even the cast skins of tarantulas. Switching gears he displayed an equally varied set of images that illustrated the diverse defensive strategies of aposematic or warningly colored caterpillars. Here we learned of caterpillar toxins, stings, and the ability of some caterpillars to forcibly eject defensive secretions over several centimeters. One of the most noteworthy aspects of the talk was that most of the 80 or more species that were used to illustrate his presentation are to be found within the city limits of Washington, D.C.

Don Davis wrapped up the meeting with slides of lichen-feeding tineid moths. The meeting was adjourned at 9:00 pm.

Delicious refreshments were generously and abundantly provided by Ralph Eckerlin.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

PUBLICATIONS FOR SALE BY THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

Miscellaneous Publications

A Handbook of the Families of Nearctic Chalcidoidea (Hymenoptera), by E. Eric Grissell and Michael E. Schauff. 85 pp. 1990 ..... $10.00

A Handbook of the Families of Nearctic Chalcidoidea (Hymenoptera): Second Edition, Revised, by E. Eric Grissell and Michael E. Schauff. 87 pp. 1997 ..... 15.00

Memoirs of the Entomological Society of Washington

Memoirs 2, 3, 7, 9, 10, 11, and 13 are no longer available.

No. 1. The North American Bees of the Genus *Osmia*, by Grace Sandhouse. 167 pp. 1939 ..... $15.00

No. 4. A Manual of the Chiggers, by G. W. Wharton and H. S. Fuller. 185 pp. 1952 ..... 15.00

No. 5. A Classification of the Siphonaptera of South America, by Phyllis T. Johnson. 298 pp. 1957 ..... 15.00

No. 6. The Female Tabanidae of Japan, Korea and Manchuria, by Wallace P. Murdoch and Hirosi Takahasi. 230 pp. 1969 ..... 15.00

No. 8. The North American Predaceous Midges of the Genus *Palpomyia* Meigen (Diptera: Ceratopogonidae), by W. L. Grogan, Jr. and W. W. Wirth. 125 pp. 1979 ..... 12.00

No. 12. The Holarctic Genera of Mymaridae (Hymenoptera: Chalcidoidae), by Michael E. Schauff. 67 pp. 1984 ..... 5.00

No. 14. Biology and Phylogeny of Curculionoidea, edited by R. S. Anderson and C. H. C. Lyal. 174 pp. 1995 ..... 25.00

No. 15. A Revision of the Genus *Ceratopogon* Meigen (Diptera: Ceratopogonidae), by A. Borkent and W. L. Grogan, Jr. 198 pp. 1995 ..... 25.00

No. 16. The Genera of Beridinae (Diptera: Stratiomyidae), by Norman E. Woodley. 231 pp. 1995 ..... 25.00

No. 17. Contributions on Hymenoptera and Associated Insects, Dedicated to Karl V. Krombein, edited by B. B. Norden and A. S. Menke. 216 pp. 1996 ..... 25.00

No. 18. Contributions on Diptera, Dedicated to Willis W. Wirth, edited by Wayne N. Mathis and William L. Grogan, Jr. 297 pp. 1997 ..... 25.00

No. 19. Monograph of the Stilt Bugs, or Berytidae (Heteroptera), of the Western Hemisphere, by Thomas J. Henry. 149 pp. 1997 ..... 18.00

No. 20. The Genera of Elaphidiini Thomson 1864 (Coleoptera: Cerambycidae), by Steven W. Lingafelter. 118 pp. 1998 ..... 12.00

No. 21. New World *Blepharida* Chevrolat 1836 (Coleoptera: Chrysomelidae: Alticinae), by David G. Furth. 110 pp. 1998 ..... 12.00

No. 22. Systematics of the North American Species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae), by John D. Pinto. 287 pp. 1999 ..... 28.00

Back issues of the Proceedings of the Entomological Society of Washington are available at $60.00 per volume to non-members and $25.00 per volume to members of the Society.

Prices quoted are U.S. currency. Postage extra except on prepaid orders. Dealers are allowed a discount of 10 per cent on all items, including annual subscriptions, that are paid in advance. All orders should be placed with the Custodian, Entomological Society of Washington, % Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0168.

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PROCEEDINGS

of the

ENTOMOLOGICAL SOCIETY

# of WASHINGTON

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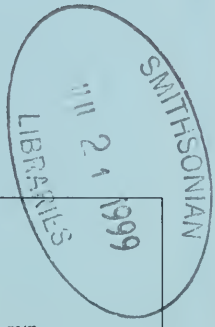

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THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

ORGANIZED MARCH 12, 1884

All correspondence concerning Society business should be mailed to the appropriate officer at the following address: Entomological Society of Washington, % Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0168.

MEETINGS.—Regular meetings of the Society are held in the Natural History Building, Smithsonian Institution, on the first Thursday of each month from October to June, inclusive, at 7:30 P.M. Minutes of meetings are published regularly in the *Proceedings*.

MEMBERSHIP.—Members shall be persons who have demonstrated interest in the science of entomology. Annual dues for members are $25.00 (U.S. currency).

PROCEEDINGS.—The *Proceedings of the Entomological Society of Washington* (ISSN 0013-8797) are published quarterly beginning in January by The Entomological Society of Washington. POSTMASTER: Send address changes to the Entomological Society of Washington, % Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0168. Members in good standing receive the Proceedings of the Entomological Society of Washington. Nonmember U.S. subscriptions are $60.00 per year and foreign subscriptions are $70.00 per year, payable (U.S. currency) in advance. Foreign delivery cannot be guaranteed. All remittances should be made payable to *The Entomological Society of Washington*.

The Society does not exchange its publications for those of other societies.

PLEASE SEE PP. 699–700 OF THIS ISSUE FOR INFORMATION REGARDING PREPARATION OF MANUSCRIPTS.

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REVIEW OF THE NEW WORLD TREEHOPPER TRIBE STEGASPIDINI (HEMIPTERA: MEMBRACIDAE: STEGASPIDINAE): I: *BOCYDIUM* LATREILLE, *LIRANIA* STÅL, AND *SMERDALEA* FOWLER

JASON R. CRYAN AND LEWIS L. DEITZ

Department of Entomology, Box 7613, North Carolina State University, Raleigh, NC 27695-7613, U.S.A. (e-mail: jrc233@email.byu.edu; lewis_dietz@ncsu.edu); (JRC) current address: Department of Zoology, Brigham Young University, Provo, UT 84602, U.S.A.

Abstract.—The tribe Stegaspidini Haupt, 1929 (Hemiptera: Membracidae: Stegaspidinae) and three included genera, *Bocydium* Latreille, *Lirania* Stål, and *Smerdalea* Fowler, are described and illustrated based on adult and nymphal morphology. *Bocydium* has 15 valid species, including ***B. duoglobum* Cryan, new species**; *Lirania* is monotypic; and *Smerdalea* has 4 valid species, including ***S. imminens* Cryan, new species**. The genus *Smerdalea* is transferred from the tribe Microcentrini to Stegaspidini; a description of the previously unknown nymph of *S. elevata* Cryan is given. Updated taxonomic keys for the tribe and for the genera *Bocydium* and *Smerdalea* are presented; complete species checklists are compiled, with synonymies, for each genus.

Key Words: Membracidae, Stegaspidini, *Bocydium, Lirania, Smerdalea,* taxonomy

Stegaspidini are unusual and often conspicuous treehoppers occurring in Mexico and throughout Central America and most of South America. Here included in this tribe are the genera *Bocydium* Latreille, *Lirania* Stål, *Smerdalea* Fowler, *Lycoderes* Germar, *Oeda* Amyot and Serville, *Stegaspis* Germar, *Flexocentrus* Goding, *Stylocentrus* Stål, and *Umbelligerus* Deitz. Whereas all members of its sister tribe Microcentrini are solitary as adults (Cryan and Deitz, in press), some stegaspidines have been observed in small aggregations of adults and nymphs (Haviland 1925a, Boulard 1979g). In addition, species of *Flexocentrus, Stegaspis,* and *Lycoderes* have been observed with ant attendants (Cryan and Deitz, in preparation). Host records currently available for Stegaspidini are restricted to the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae.

The primary goal of this work is to review the tribe Stegaspidini at the generic level, based on comparative morphology. Keys for the identification of various stegaspidine taxa were outdated or nonexistent, and are here modernized. A summary of known distribution and biological data for the included taxa is provided, and for genera where sufficient material and information were available, species level revisions are presented. In all other cases, an updated species checklist is compiled following the generic description. The tribe will be reviewed in a series of three publications, with the present paper including a redescription of the tribe Stegaspidini, as well as treatments of the genera *Bocydium, Lirania,* and *Smerdalea.*

Amyot and Serville (1843a) recognized the group by the vernacular name "Bocydides" and Goding (1926e) called the same

group "Acuminatini" (a *nomen nudum*). Haupt (1929c) established the subfamily Stegaspidinae (incorrectly spelled as Stegaspinae) to include four new tribes: Platycentrini, Stegaspidini (as Stegaspini), Stylocentrini, and Oedini. Many of the genera in these tribes had previously been placed in the membracid subfamily Centrotinae based on the exposed scutellum—Metcalf and Wade's (1965a) catalog listed Haupt's Oedini, Lycoderini, and Stegaspidini (as Stegaspini) as tribes of Centrotinae. Hamilton (1971b) moved seven "stegaspidine" genera (including *Bocydium, Flexocentrus, Smerdalea,* and *Stylocentrus*) to the family Aetalionidae under the subfamily "Stylocentrinae," but referred *Stegaspis* to the Membracinae (Membracidae).

Deitz (1975a) redefined the subfamily Stegaspidinae (as Stegaspinae), including the nominotypical tribe Stegaspidini (as Stegaspini, with the synonyms Stylocentrini Haupt 1929c, Stylocentrinae Haupt 1929c [*sensu* Hamilton 1971b], Oedini Haupt 1929c, Lycoderini Metcalf and Wade 1965a, and Bocydides Amyot and Serville 1843a). Based on certain wing features, Shcherbakov (1981a, b, 1982a, b) included *Stylocentrus* (in Stylocentrini), *Bocydium,* and *Stegaspis* in Aetalionidae. Deitz (1983b) emended the spelling of the subfamily and its nominotypical tribe to Stegaspidinae and Stegaspidini, respectively.

Selected stegaspidine genera have been included in various phylogenetic analyses of the Membracidae and related families. Strümpel (1972a) proposed a phylogeny of the Membracidae based primarily on pronotal structure, concluding that members of Stegaspidini arose from within the Centrotinae. Sakakibara's (1979) unpublished cladistic analysis of the Membracidae found that *Smerdalea* formed a clade with *Stylocentrus,* in Stegaspidini, rather than in Microcentrini where it had been placed. Finally, a recent phylogenetic analysis of the Membracoidea suggested that Stegaspidinae, consisting of the sister groups Microcentrini (*sensu* Deitz 1975a) and Stegaspidini (*sensu* Deitz 1975a, less *Euwalkeria* Goding), is a basal lineage of the family Membracidae (Deitz and Dietrich 1993a, Dietrich and Deitz 1993a); those works did not attempt to resolve relationships within the Stegaspidinae.

Metcalf and Wade's (1965a) catalog should be consulted for other references to the literature on members of Stegaspidini prior to 1956. Citations of membracid literature used in this work conform to the use of letter designations to indicate chronology of publication within a single year, initiated in Metcalf and Wade (1963a), and continued by later workers (Deitz and Kopp 1987a, Deitz 1989a, McKamey 1998a).

Deitz (1975a) distinguished Stegaspidini from related tribes based on diagnostic characters of the forewing (venation simple, not reticulate, with one m-cu crossvein), the metathoracic leg (femur lacking longitudinal row of cucullate setae; tibia triquetrous or foliaceous, lacking cucullate setae in row I, rows I and III, or rows I, II, and III), and the abdominal terga (lacking middorsal tuberosities). The definition of the tribe is here modified; as detailed below, the tribe Stegaspidini is now defined by the following combination of characters: forewing lacking reticulate venation, with one r-m and one m-cu crossvein, and vein R_{2+3} fused basally with R_1; metathoracic femur lacking cucullate setae; and male lateral plates are free and lacking posteroapical hooks or fused to the pygofer.

Materials and Methods

Stegaspidine treehopper specimens were obtained through requests to New World and European collections and by a note in the *Tymbal,* an Auchenorrhyncha newsletter (Cryan and Bartlett 1994a). An endeavor was made to locate and examine the type species of all included genera, as well as the type material for many of the included species. The only genus not examined during this work was *Lirania,* for which descriptions and illustrations are based on those by Deitz (1975a).

The following codens are used in this work to refer to the collections in which relevant specimens are located or have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†).

AMNH: American Museum of Natural History, New York, New York, USA.

BMNH: Department of Entomology, The Natural History Museum, London, United Kingdom.

BPBM: Department of Entomology, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

CISC: Essig Museum of Entomology (California Insect Survey Collection), University of California, Berkeley, California, USA.

CNCI: Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Research Branch, Ottawa, Ontario, Canada.

GMPC†: Gérard Moragues Personal Collection, Marseille, France.

IZAV: Instituto de Zoologiá Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.

MNHN: National Collection of Insects, Muséum National d'Histoire Naturelle, Paris, France.

MZLU: Museum of Zoology, Lund University, Helgonavägen, Lund, Sweden.

NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.

SEMC: Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

SHMC†: S. H. McKamey Collection, currently at the United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, % National Museum of Natural History, MRC-168, Washington, D.C., USA.

TKWC†: T. K. Wood Collection, currently at the Department of Entomology and Applied Ecology, University of Delaware, Newark, Delaware, USA.

USNM: Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

ZMUH: Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg, Germany.

Observations and illustrations were made using a Leitz® stereoscopic microscope (at 8 to 144× magnification) with an attached camera lucida. Measurements were taken with an ocular micrometer at 8× magnification. Genitalia dissections were prepared as described by Deitz (1975a); non-type specimens dissected during this work bear labels indicating "Cryan Research" numbers. Genitalia, and occasionally legs, were immobilized for illustration by imbedding part of the structure in a drop of boric acid ointment in glycerine. After examination and illustration, the dissected structures were placed inside the abdomen, which was then deposited in a microvial (either glass with a cork stopper or polypropylene with a rubber stopper) containing a small amount of glycerine for preservation. The vials were then pinned with their appropriate specimens.

A Philips 505T Scanning Electron Microscope was used to examine the pronota of selected stegaspidine species. The treehoppers so examined are pinned non-type and type specimens. Due to the scientific value and rarity of many of these specimens, they were scanned without the usual metal coating, using custom made specimen mounts (stubs) to accommodate the insect

pin. Electron microscopic examination without metal coating on the specimens necessitated the use of low voltage settings (≈ 5 kv) to reduce charging effects.

New species are described by the first author; all type specimens designated in this work are conspicuously labeled with colored labels (white with red outline for holotypes and white with blue outline for paratypes). Institutions where type specimens are deposited are listed in the relevant "Material examined" sections, along with quotations of label information. Where particular labels are quoted, the information from each label is enclosed in quotation marks, and individual lines within a label are separated by a virgule (/).

Distribution records are presented in two ways. In cases where only a generic review is given, all countries in which species of that genus have been found are listed under the heading "Range." For cases where species are treated individually, a separate "Distribution" section lists the countries where that species has been found. Following each distribution record is either a coden or a superscript number. Codens refer to a collection that includes specimens validating that record (only one collection is listed in most cases, although multiple collections may have specimens validating the distribution record). Superscript numbers document records from: [1]Metcalf and Wade (1965a), not confirmed in this work and should be used with caution, as some may be based on misidentified species; and [2]Cryan and Deitz (1995a), codens not included here to avoid redundancy. Unverified distribution records from Metcalf and Wade (1965a) should be used with caution, as some may be based on misidentified specimens.

Following the description of each genus and species treated in this work are brief remarks concerning items of interest peculiar to that taxon. Included in these sections are any references to host-plant identities, biology and life-history notes, collection and habitat information, and hypotheses concerning the relationships of the taxa to other groups.

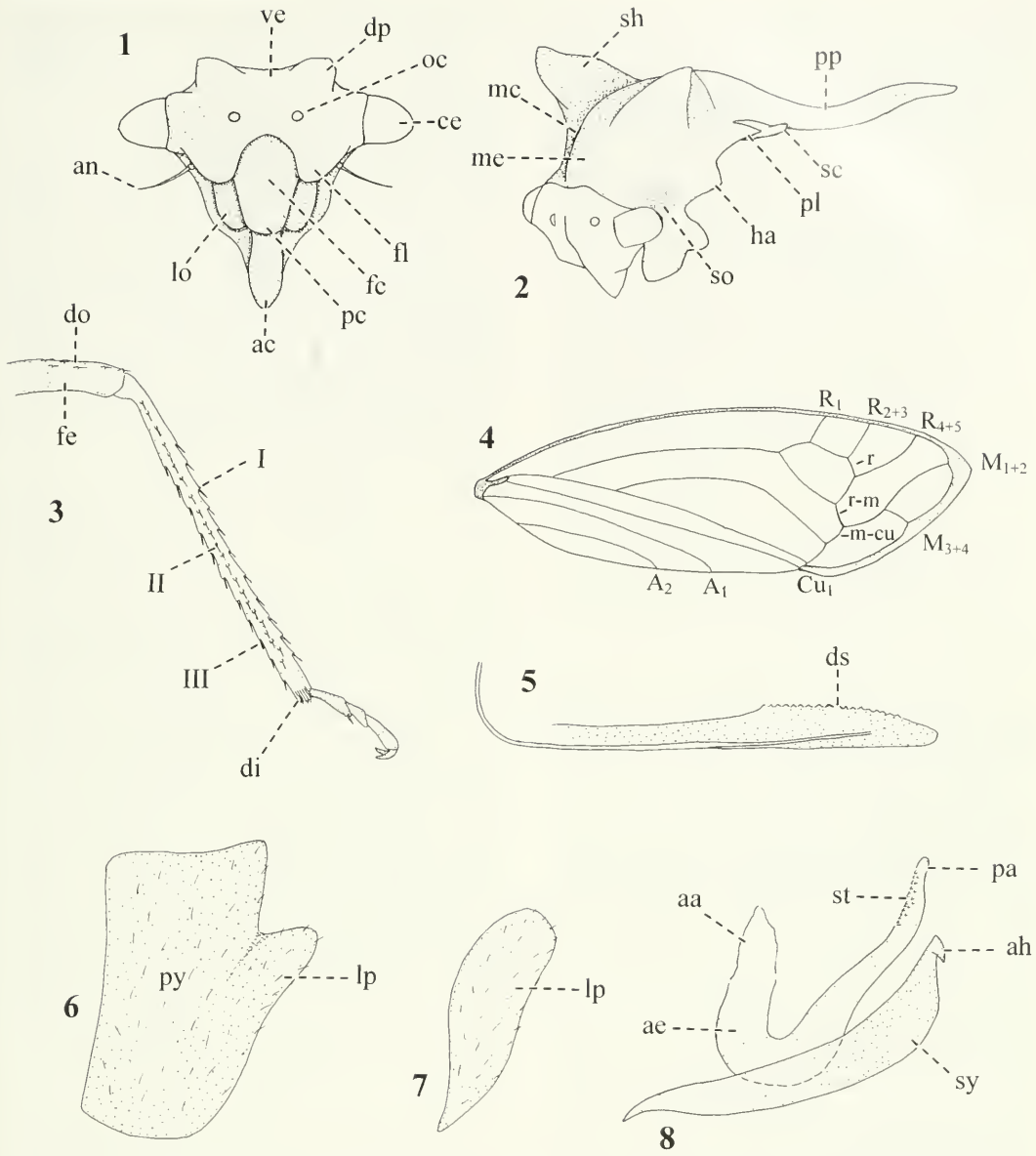
Morphological Characters

The taxonomically important morphology for the subfamily Stegaspidinae, including Stegaspidini, is illustrated in Figs. 1–8. The terminology used in this work follows recent usage for Membracidae (Deitz 1975a—general morphology; McKamey and Deitz 1991c—morphology of the pronotum; Capener 1962a—supraocular callosities, centro-ocular line).

Taxonomically useful features of the stegaspidine head (Fig. 1) include the relative size of the dorsal projections, location of the ocelli relative to the centro-ocular line, the nature (size and shape) of the foliate lobes, and the shape of the frontoclypeus (uni- or trilobed). In addition, many species of Stegaspidini have the compound eyes and ocelli sessile, not stalked (Figs. 19–20), whereas the compound eyes and ocelli of some species are stalked (Fig. 23; Deitz 1975a fig. 40C).

The thorax, with the legs and wings, holds many characters informative at a variety of taxonomic levels. These include the structure of the pronotum (Fig. 2; shape of the metopidial region suprahumeral horns, posterior process, and humeral angles), nature of the scutellum (Figs. 2, 13, 20; apex emarginate or acuminate), shape of the tibiae (Fig. 3, not foliaceous; Deitz 1975a: fig 39d, foliaceous), chaetotaxy of the metathoracic leg (Fig. 3; presence or absence of cucullate setae on the femur and in the three enlarged setal rows of the tibia), and forewing structure and venation (Fig. 4; extent of wing that is coriaceous, number and location of crossveins, and branching patterns of vein R). Other thoracic features include the surface sculpturing of the pronotum (Figs. 28–30; shape of ultrastructural pits and associated setae) and the presence of supraocular callosities.

Some descriptions include mention of the metopidium (the pronotal region dorsad of the anterior 'face' of the head). In some



Figs. 1–8. Diagrammatic Morphology of Stegaspidini. 1, Head, anterior aspect (face). 2, Head, pronotum, and scutellum, anterolateral aspect. 3, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 4, Right forewing. 5, Female second valvulae, lateral aspect. 6, Male pygofer and posterior lobe (fused lateral plate), left lateral aspect. 7, Male left lateral plate (free, not fused), lateral aspect. 8, Male aedeagus and left style, lateral aspect. Abbreviations: $A_{\#}$ = anal veins; aa, anterior arm; ac = anteclypeus; ae aedeagus; ah, apical hook; an = antenna; ce, compound eye; Cu_1 = cubital vein; di = distal setal row; do = dorsal setal row; dp = dorsal projection; ds = dorsal serrations; fc = frontoclypeus; fe = femur; fl = foliate lobe; ha = humeral angle; lo = lorum; lp = lateral plate; $M_{\#}$ = medial vein(s); mc = median carina; me = metopidium; oc = ocellus; pa = posterior arm; pc = frontoclypeus; pl = posterolateral process; pp = posterior pronotal process; py = pygofer; $R_{\#}$ = radial vein(s); sc = scutellum; sh = suprahumeral horn; so = supraocular callosity; st = subapical teeth; sy = style; ve = vertex; I, II, III = enlarged setal rows.

species, the metopidium is not elevated (Fig. 24), sloping smoothly to the posterior pronotal process; in other species (Figs. 11, 13) the metopidium is elevated, often bearing the suprahumeral horns and the posterior pronotal process high above the body of the insect. We consider any pronotal extensions located above the humeral angles to be suprahumeral horns. Thus, the stalked bulbs of *Bocydium* spp. (Figs. 9, 11, 13), the unbranched triquetrous processes of *Lycoderes* spp. (Deitz 1975a: fig. 40T), and the sometimes trifurcating horns of *Smerdalea* spp. (Fig. 24) are homologous. The location and structure of suprahumeral horns vary greatly within the tribe Stegaspidini, and even within some genera; nevertheless, the nature of these pronotal extensions usually provides excellent taxonomic features at the specific and generic levels.

Abdominal characters center on the male and female genitalia. Characters of the female genitalia include shape and degree of serration of the second valvulae (Fig. 5). Valuable features of the male genitalia include the degree of fusion and structure of the lateral plates (fused to pygofer completely or basally [Fig. 6], or entirely free [Fig. 7]), structure of the styles (Fig. 8; width and shape of the apical hook), and structure of the aedeagus (Fig. 8; width, shape, and surface features of anterior face of posterior arm). All known stegaspidine nymphs have setose abdominal lamellae and emarginate wingpads (Figs. 10, 22).

Measurements recorded include the total length of the body with wings in repose (from head to apex of forewings), length of the pronotum, width between the humeral angles, length of the forewings, and the maximum width of the centro-ocular line (maximum width of head across eyes).

Tribe Stegaspidini Haupt 1929c

Bocydides Amyot and Serville 1843a: 551 [a vernacular name].

Acuminatini Goding 1926e: 297 [*Nomen nudum*]

Stegaspini Haupt 1929c: 228. Emended to Stegaspidini Haupt 1929c: Deitz 1983b: 856.

Stylocentrini Haupt 1929c: 228.

Stylocentrinae Haupt 1929c: 228.

Oedini Haupt 1929c: 228.

Lycoderini Metcalf and Wade 1965a: 45.

Diagnosis.—Species of Stegaspidini have the forewing with 1 r-m and 1 m-cu (usually basad of the fork of vein M) crossvein and vein R_{2+3} fused basally with R_1; the ♂ lateral plates either free (without posteroapical hooks) or basally fused to the pygofer.

Adult.—*Dimensions* (mm): Total length 3.2–13.8. *Structure: Head:* Compound eyes and ocelli stalked (Fig. 12) or not (Fig. 19); ocelli above centro-ocular line (exception: ocelli of *Smerdalea* on or below centro-ocular line); dorsal projections generally small (with some exceptions). *Thorax: Pronotum*: Middorsal crest present, extending over partial or entire length of pronotum; posterior process extending over scutellum (dorsally concealing scutellum or not; scutellum usually not concealed laterally except in at least one species—*Lycoderes phasianus* Fowler). *Pronotal surface sculpturing* (Figs. 28–30): Punctate; generally, one seta associated with each pit; surface smooth or tuberculate. *Legs:* Metathoracic femur usually lacking cucullate setae (at least, dorsal band of cucullate setae absent); metathoracic tibiae foliaceous (Deitz 1975a: fig. 39D) or not (Fig. 14), with cucullate setae in rows II and (in some species) III. *Forewing* (Fig. 4): 1 r-m and 1 m-cu crossvein present. *Genitalia:* ♀ 2nd valvulae slightly broadened or of uniform width, with dorsal serrations on distal region; ♂ lateral plate either free, without hook, or basally fused to pygofer.

Late-instar nymph.—Body slightly flattened dorsoventrally; pronotum with or without carinae or horns, often produced into a laterally compressed hump; all tibiae foliaceous; abdominal segments 4–8 with platelike lateral lamellae.

Range.—Argentina to Mexico, including Trinidad.

Remarks.—As stated by Deitz (1975a), the reduction in forewing venation and in numbers of metathoracic tibial rows of cucullate setae in Stegaspidini indicate that this group is derived in more features than is its sister tribe, Microcentrini. In addition, the elaborate pronota of most Stegaspidini suggest more specialized forms of crypsis than seen in most Microcentrini (Cryan and Deitz, in press). The conspicuous, chalazae-fringed abdominal lamellae of Stegaspidini nymphs (also evident in Microcentrini) are similar to those of the nymphs of Nessorhininae, Procyrtini (Darninae), and most Centrotinae (S. H. McKamey, personal communication).

Little is known about the biology and life histories of these treehoppers. Members of Stegaspidini are recorded from the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae. Microbial endosymbionts have been recorded from *Bocydium globulare, Lycoderes galeritus,* and *L. mitratus* (Müller 1949a, Buchner 1953a). Haviland (1925a) observed adults of *Flexocentrus felinus* [as *Centruchoides felinus*] and *Stegaspis fronditia* [as *S. galeata*] with ant attendants. Additional information is recorded for some species (see individual descriptions).

Key to the Genera of Adult Stegaspidini

1. Tibiae not foliaceous; hind tibia with cucullate setae in enlarged setal rows I, II, and/or III enlarged setal rows 3
– All tibiae foliaceous; hind tibia with cucullate setae in enlarged setal row II only, or absent 2
2. Suprahumeral horns absent (Fig. 20); hind tibia without cucullate setae . . . . . *Lirania* Stål
– Suprahumeral horns present, pyramiform (Deitz 1975a: fig. 40Q); hind tibia with cucullate setae in row II . . . . . *Flexocentrus* Goding
3. Metopidium gibbous, not elevated 5
– Metopidium elevated, usually laterally compressed 4
4. Cranial foliate lobes not extending over frontoclypeus (Fig. 1); suprahumeral horns present, though sometimes very small at apex of elongate dorsal metopidium (Deitz 1975a: fig. 40T); posterior pronotal process variable . . . . . *Lycoderes* Germar
– Cranial foliate lobes extending over frontoclypeus (Deitz 1975a: fig. 40B), suprahumeral horns absent (Deitz 1975a: fig. 40U); posterior pronotal process laterally compressed, leaflike (Deitz 1975a: fig. 40U) . . . . . *Stegaspis* Germar
5. Forewing with vein A_1 partially confluent with claval suture and distal m-cu crossvein distad of fork of vein M (Fig. 26) . . *Smerdalea* Fowler
– Forewing with vein A_1 entirely separate from claval suture (Fig. 4) and distal m-cu crossvein basad of fork of vein M 6
6. Head with dorsal projections indistinct or absent (Fig. 12); ♂ lateral plates free, without posteroapical hooks (Figs. 7, 17) 7
– Head with distinct dorsal projections (Deitz 1975a: figs. 40E–F); ♂ lateral plates fused to pygofer (Fig. 6) 8
7. Posterior pronotal process inflated, balloonlike, with reticulate venation (Deitz 1975a: fig. 40S); suprahumeral horns short, digitate or absent (Deitz 1975a: fig. 40S) . . . . . *Oeda* Amyot and Serville
– Posterior pronotal process simple, spinelike; suprahumeral horns long, branched, bearing inflated bulbs (Fig. 11) . . . . . *Bocydium* Latreille
8. Suprahumeral horns unbranched (Deitz 1975a: fig. 40O); hind tibia with cucullate setae in row II and in distal ⅓ of row III (row I with 1–3 cucullate setae distally) . . . . . *Stylocentrus* Stål
– Suprahumeral horns branched (Deitz 1975a: fig. 40P); hind tibia with cucullate setae in rows II and III or II only . . *Umbelligerus* Deitz

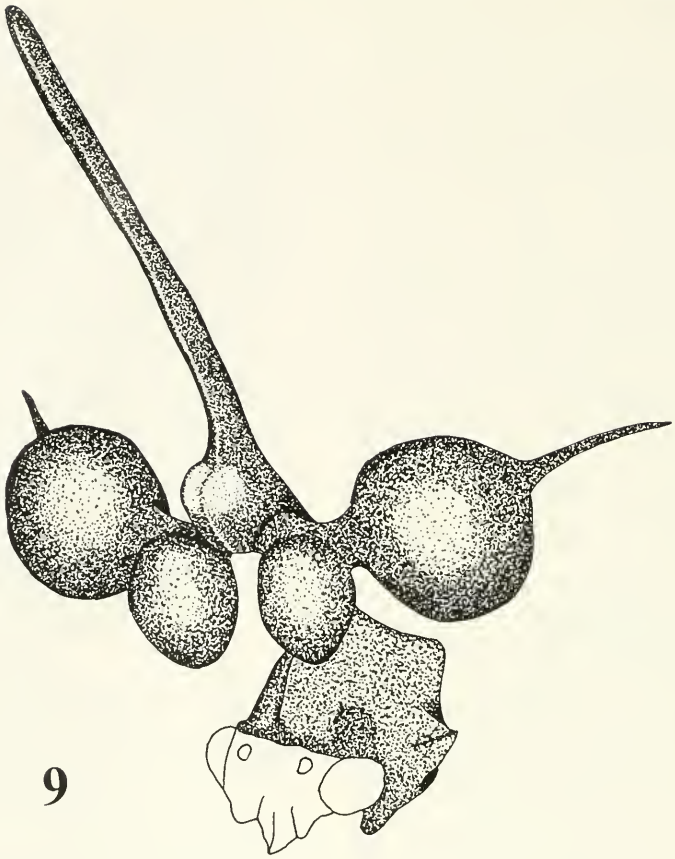
Genus *Bocydium* Latreille, 1829a

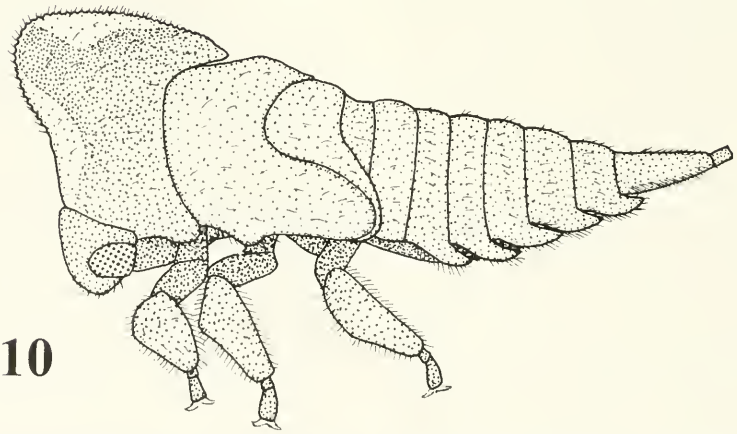
Bocydium Latreille 1829a: 219. Type species: *Centrotus globularis* Fabricius 1803a by subsequent designation of Blanchard 1849c: 614.

Sphaeronotus de Laporte 1832b: 229. Type species: *Centrotus globularis* Fabricius 1803a, by original designation.

Diagnosis.—Species of *Bocydium* are easily recognized by the inflated bulbs on the suprahumeral horns.

Adult.—*Dimensions* (mm): Total length 4.6–7.5. *Structure: Head* (Fig. 12): Dorsal projections small or absent; compound eyes and ocelli not stalked; frontoclypeus weakly trilobed. *Thorax: Pronotum* (Figs. 9, 11, 13): Slender suprahumeral horns (bearing inflated bulbs [lobes] of various sizes,





Figs. 9–10. *Bocydium* species. 9, *B. amischoglobum* (anomolous specimen), head, pronotum, and scutellum, anterolateral aspect. 10, *B. rufiglobum*, late-instar nymph, lateral aspect.

shapes, and numbers) and simple, spinelike posterior process arising from central pronotal stalk (elevated metopidium). *Pronotal surface sculpturing* (Fig. 28): Punctate, each pit associated with 1 long, narrow seta; surface finely tuberculate between pits. *Legs* (Fig. 14): Tibiae simple, not foliaceous; metathoracic tibia with cucullate setae in rows II and III only. *Forewing* (Fig. 15): 1 r-m and 1 m-cu crossvein present; r-m crossvein basad of branch of vein M. *Genitalia*: ♀ 2nd valvulae (Fig. 16) slightly broadened at midlength, with dorsal serrations on distal half; ♂ lateral plate (Fig. 17) free, without posteroapical hook.

Late-instar nymph.—Known only for *B. rufiglobum* Fairmaire (Fig. 10) and *B. cubitale* Richter (1955a: fig. 6B): pronotum laterally flattened, metopidium vertically produced into median horn with darker internal structure visible through integument; tibiae foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 4–8, fringed with setae.

Range.—Paraguay[1]; Bolivia [AMNH]; Brazil [NCSU]; Peru [NCSU]; Ecuador [USNM]; Colombia [ZMUH]; French Guiana [CNCI]; Suriname [ZMUH]; Guyana [NCSU]; Venezuela [IZAV]; Costa Rica [TKWC]; Trinidad [USNM].

Material examined.—16 specimens from AMNH (including holotype of *Bocydium bullifera* Goding [♀] with labels: "Bolivien," "Matausch Coll./Ac. 4883," "A. Mus. Nat. Hist./Dept. Invert. Zool./No.," "Bocydium/S. Bol.," "Deitz Research/72-81e ♀," "Bocydium/bulliferum/type Goding.," and "HOLOTYPE/BOCYDIUM/BULLIFERA/Goding"); 29 from BMNH; 6 from BPBM; 1 from CISC; 8 from CNCI; 18 from IZAV; 5 from MZLU; 82 from NCSU; 1 from SEMC; 31 from SHMC; 11 from TKWC; 32 from USNM; 104 from ZMUH (including Cryan Research #93-353a ♀).

Remarks.—Funkhouser (1951a) characterized *Bocydium* as "one of the most remarkable of all of the genera of the Membracidae and with structures as curious and bizarre as those of any insect family . . . surely from the signs which are displayed above their heads, these must be the pawnbrokers among insects." Members of this genus are usually small, dark insects with a delicate appearance. Although Poulton (*in* Buckton 1903b) advanced the possibility that the pronota mimic Neotropical seeds or small, spiny fruit, the actual function of the peculiar pronotal structures is unknown, as are the life histories of many of the species. Richter (1955a) reported *B. astilatum* and *B. nigrofasciatum* from an unidentified plant belonging to the Melastomataceae and *B. cubitale* from *Pithocarphya poeppigiana* (Asteraceae); Wood (1984a) reported *B. globulare* on *Miconia* sp. (Melastomataceae). McKamey (personal communication) collected *Bocydium* on *Vismia* sp. (Guttiferae); Haviland (1925a) reported that *B. globulare* usually occurs only a few feet above the ground, feeding on the undersides of leaves. Adults of this genus seem to be solitary, although multiple specimens have been taken from branches of the same tree (Wood 1984a).

Species of *Bocydium* are frequently illustrated as examples of strange treehoppers. Illustrations of *Bocydium* sp., prob. *globulare*, appear in publications by Vignon (1930a), Heikertinger (1954a), Seitz (1951a), and Suchantke (1983a). A photograph of *Bocydium* sp. (as "*B. rufiglabrum*" in the figure caption) was published by Parenti (1971a, 1972a), whereas Klausnitzer (1987a) published a picture of *B. amischoglobum* (as "*B. rufiglobum*" in the figure caption) and Boulard (1986a) published a photograph of *B. globulare*. Strümpel (1983a) published a scanning electron micrograph of the full body of *B. globuliferum*.

An unusual specimen of *B. amischoglobum* (from ZMUH, bearing label "Cryan Research #93-353a ♀") is illustrated here (Fig. 9). The normal condition for this species (and all others in this genus) is for the posterior pronotal process to extend posteriorly. This aberrant individual has the pos-

terior process extending dorso-anteriorly, much like a unicorn.

Sakakibara (1981c) published a partial revision of this genus; because of this recent work, the treatment of *Bocydium* here is limited to the following: the description of one new species of *Bocydium*; a taxonomic key, modified from Sakakibara (1981c) to include all *Bocydium* species (original descriptions of six species not examined in the present work did not give diagnoses sufficient for unqualified taxonomic separation; thus, those species are grouped as potential identities in the key, below); and a synonymic checklist of the species.

Bocydium duoglobum Cryan, new species

(Figs. 11–18, 29)

Type locality.—Barbacoas, Nariño, Colombia.

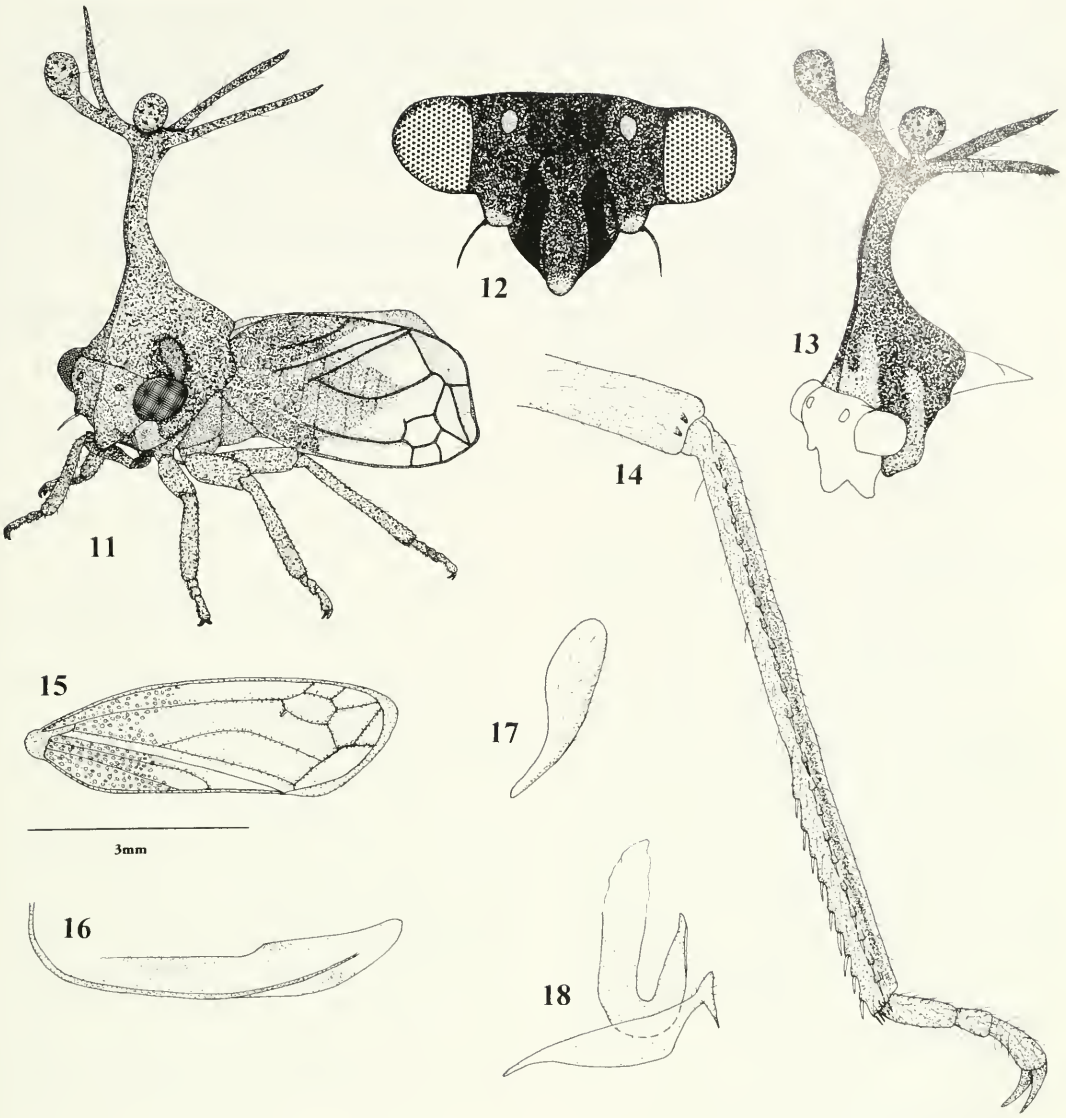
Diagnosis.—*Bocydium duoglobum* has each suprahumeral horn with only a single, stalked bulb (Figs. 11, 13). The suprahumeral horns and the posterior pronotal process project obliquely upwards from a long, posteriorly curved stalk.

Adult.—*Dimensions* (mm): Total length ♀, ♂ 4.6–4.8; width between humeral angles ♀ 1.4, ♂ 1.2–1.4; pronotal height ♀ 2.1, ♂ 1.9–2.9; wing length ♀ 4.1, ♂ 3.6–4.0; maximum width of head across eyes ♀ 1.4, ♂ 1.3–1.4. *Coloration:* Head and thorax dark brown, nearly black, with or without pale wax patterns; abdomen and legs tan; wings hyaline with brown patches. *Structure: Head:* Face (Fig. 12) sparsely setose; with or without waxy secretions in defined patterns; eyes not stalked; ocelli on slightly raised tubercles; dorsal projections small, separated by distance equal to separation of ocelli; dorsal transverse ridge small; post-frontal sutures obscure; frontoclypeus produced ventrally. *Thorax: Pronotum* (Fig. 13): With short setae, except for suprahumeral horns and posterior process, which bear sparse, long setae; with or without waxy secretions in defined patterns; supraocular callosities obscure; humeral angles somewhat produced, but not acute; dorsal carina obscure; suprahumeral horns each with 2 branches: lateral branches simple, spinelike, and anterior branches each bearing a stalked bulb; posterior process simple, spinelike, of roughly equal length to lateral branches of suprahumeral horns; suprahumeral horns and posterior process arise from long, posteriorly curved pronotal stalk at approximately same point, then project obliquely upwards; internally, suprahumeral horns divided into 3 hollow tubes: a large center tube flanked by 2 smaller tubes (Fig. 29). *Pronotal surface sculpturing* (Fig. 29): Metopidium punctate, each pit associated with 1 long, narrow seta; pits on pronotal stalk often oblong, slitlike (rather than round); surface of suprahumeral horns and posterior pronotal process tuberculate. *Scutellum* (Fig. 13): Short; elevated anteriorly, then flattened to acuminate apex; darkly pigmented anteriorly, with distal area bright yellow. *Legs* (Fig. 14): Metathoracic femur with 2 or 3 dorsal cucullate setae apically; metathoracic tibia with cucullate setae only in setal rows II and III; row II with cucullate setae throughout, row III with cucullate setae in apical ⅓. *Forewing* (Fig. 15): Basal ⅓ thickened, punctate (except area between claval suture and vein Cu), obscuring vein A_2; crossvein r-m_1 absent or an incomplete stub. *Genitalia:* ♀: 2nd valvulae (Fig. 16) abruptly broadened at about ⅔ of their length, tapering to dorsally curved apex; dorsal ridge of broadened area without distinct serrations; ♂: Lateral plates (Fig. 17) free, without apical hook; styles (Fig. 18) hooked apically (resembling the bill of a bird); aedeagus (Fig. 18) strongly U-shaped, tapering apically, anterior face of posterior arm not denticulate.

Late-instar nymph.—Unknown.

Distribution.—Colombia: Nariño [BMNH].

Material examined.—Holotype: [♂] [BMNH], with labels "COLOMBIA: Na-/



Figs. 11–18. *Bocydium duoglobum*, structures of the holotype (genitalia illustrated from the paratypes). 11, Full body, anterolateral aspect. 12, Head, anterior aspect (face). 13, Head, pronotum, and scutellum, anterolateral aspect. 14, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 15, Right forewing. 16, Female second valvulae, lateral aspect. 17, Male left lateral plate, lateral aspect. 18, Male aedeagus and left style, lateral aspect.

rino, Barbacoas/5.I.1975/M. Cooper/B.M. 1975-33" and "HOLOTYPE ♂/*Bocydium/duoglobum*/J. R. Cryan." Paratype: [♀, dissected, with posterior pronotal process broken; BMNH], with labels "COLOMBIA:/ Narino, Barba-/coas.19-21.vii.1974/M. Cooper/B.M. 1974-548" and "PARATYPE ♀/*Bocydium/duoglobum*/J. R. Cryan." Other specimens: 2 ♂ (1 with missing head and pronotum, and 1 [dissected] with wings missing) from BMNH (including Cryan Research #94-253a ♂).

Remarks.—*Bocydium duoglobum* resembles *B. germarii* Guérin-Méneville in that each suprahumeral horn bears only one bulb, but *B. duoglobum* differs in having the bulbs stalked. Also, the lateral branches of the suprahumeral horns are simple (those

of *B. germarii* bear reduced bulbs), and the suprahumeral horns and the posterior pronotal process rise obliquely from the pronotal stalk (in *B. germarii*, they extend away from the pronotal stalk at nearly 90° angles). *Bocydium duoglobum* is much darker than *B. germarii*.

The specific name is a combination of the Latin terms "duo" (meaning "two") and "globum" (from "globus," meaning "ball or sphere"), referring to the structure of the suprahumeral horns.

Key to Species of Adult *Bocydium* (Modified from Sakakibara 1981c)

1. Lateral branches of suprahumeral horns each with, at most, a single globe 2
– Lateral branches of suprahumeral horns each with two globes . . . *B. sexvesicatum* Sakakibara
2. Lateral globes smaller than the anterior globes, or lacking 3
– Lateral globes equal to or larger than the anterior globes 5
3. Anterior globes normal, lateral globes reduced 4
– Both anterior and lateral globes reduced or absent . . . . . *B. germarii* Guérin-Méneville
4. Lateral globes fusiform . . . . . *B. sphaerulatum* Sakakibara
– Lateral globes lacking entirely (Fig. 11) . . . . . *B. duoglobum* Cryan, new species
5. Anterior globes petiolate 6
– Anterior globes not petiolate (Fig. 9) . . . *B. amischoglobum* Sakakibara, *B. astilatum* Richter, *B. cubitale* Richter, or *B. bulliferum* Goding
6. Lateral globes noticeably larger than anterior globes 7
– Lateral globes subequal to anterior globes . . 8
7. Lateral globes ellipsoidal in outline . . . . . *B. rufiglobum* Fairmaire
– Lateral globes more or less triangular in outline . . . . . *B. anisobullatum* Sakakibara
8. Maximum distance between lateral globes smaller than double the width between humeral angles 9
– Maximum distance between lateral globes larger than double the width between humeral angles . . . . . *B. globulare* (Fabricius)
9. Lateral spines longer than the diameter of the lateral globes; coloration generally black . . 10
– Lateral spines shorter than the diameter of the lateral globes; coloration generally chestnut-brown . . . . . *B. racemiferum* Sakakibara and *B. nigrofasciatum* Richter
10. ♀ subgenital plate normal; ♂ subgenital plate also normal, but with long hairs . . . . . *B. globuliferum* (Pallas)
– ♀ subgenital plate bilobed; ♂ subgenital plate substantially lengthened, outwardly curved, and with short hairs . . . . . *B. tintinnabuliferum* Lesson

Species Checklist of *Bocydium*

amischoglobum Sakakibara
Bocydium amischoglobum Sakakibara 1981c: 825.

anisobullatum Sakakibara
Bocydium anisobullatum Sakakibara 1981c: 825.

astilatum Richter
Bocydium astilatum Richter 1955a: 278.

bulliferum Goding
Bocydium bullifera Goding 1930b: 4.

cubitale Richter
Bocydium cubitale Richter 1955a: 280.

duoglobum Cryan, **new species**

germarii Guérin-Méneville
Bocydium germarii Guérin-Méneville 1844a: 366.
Bocydium germari: Fairemaire 1846b: 509. Unjustified emendation.

globulare (Fabricius)
Centrotus globularis Fabricius 1803a: 16.
Membracis globularis: Latreille 1818c: 123.
Bocydium globulare: Latreille 1829a: 219.
Sphaeronotus globularis: de Laporte 1832b: 229.

globuliferum (Pallas)
Cicada globulifera Pallas 1766a: 187.
Cicada globulare [sic]: Blanchard 1840a: 184.
Bocydium globuliferum: Walker 1851a: 601.

nigrofasciatum Richter
Bocydium nigrofasciatum Richter 1955a: 273.

racemiferum Sakakibara
Bocydium racemiferum Sakakibara 1981c: 827.

rufiglobum Fairmaire
Bocydium rufiglobum Fairmaire 1846b: 508.
sexvesicatum Sakakibara
Bocydium sexvesicatum Sakakibara 1981c: 823.
sphaerulatum Sakakibara
Bocydium sphaerulatum Sakakibara 1981c: 826.
tintinnabuliferum Lesson
Bocydium tintinnabuliferum Lesson 1832a: [1].
Bocydium glomeriferum Germar 1835a: 260.
Bocydium globiferum [sic] Blanchard 1840a: 184.
Lycoderes tintinnabuliferum: Heymons 1926a: [I].
Bocydium tintinnabuliferum: Funkhouser 1927f: 350.

Genus *Lirania* Stål 1862e

Lirania Stål 1862e: 36. Type species: *Lirania bituberculata* Stål 1862e: 36, by original designation and monotypy.

Diagnosis.—*Lirania* is unique among Stegaspidinae in entirely lacking cucullate setal rows on the metathoracic tibiae.

Adult.—*Structure: Head:* Dorsal projections distinct. *Thorax: Pronotum:* Suprahumeral horns absent; posterior pronotal process long, unbranched. *Scutellum:* Apex emarginate. *Legs:* Pro- and mesothoracic tibiae foliaceous; metathoracic leg lacking cucullate setae. *Forewing:* Vein R_{2+3} fused basally with R_1; r-m crossvein distad of fork of vein M.

Range.—Brazil.

Remarks.—The etymology of the generic name was not described by Stål (1862e), although it may be based, in part, on the Latin "*lira,*" meaning "a ridge."

Lirania bituberculata Stål 1862e (Figs. 19–21)

Lirania bituberculata Stål 1862e: 36.

Type locality.—Rio de Janeiro, Brazil.

Diagnosis.—*Lirania bituberculata* has a simple posterior pronotal process but lacks suprahumeral horns and cucullate setal rows on all the metathoracic tibiae.

Adult ♀.—*Structure: Head* (Fig. 19): Dorsal projections distinct; eyes neither stalked nor prominent; frontoclypeus trilobed. *Thorax: Pronotum* (Fig. 20): Middorsal carina present; suprahumeral horns absent; posterior pronotal process expanded midway, tapering to acuminate apex. *Scutellum* (Fig. 20): Flat for entire length; apex emarginate. *Legs:* Pro- and mesothoracic tibiae foliaceous; metathoracic femur and tibia lacking cucullate setae in all rows. *Forewing* (Fig. 21): Apical margin rounded; vein R_{2+3} fused basally with R_1; 1 r-m and 1 m-cu crossvein present (r-m crossvein distad of fork of vein M). *Genitalia:* Not examined. ♂: Unknown.

Late-instar nymph.—Unknown.

Distribution.—Brazil: São Paulo[1].

Material examined.—None.

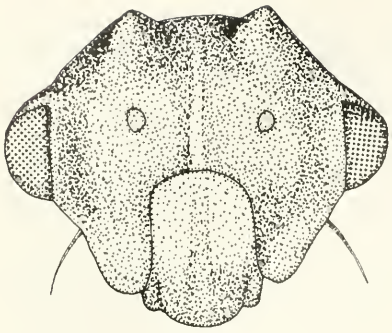
Remarks.—Although no specimens of *Lirania bituberculata* were examined in this work, Deitz (1975a) examined the lectotype and illustrated the forewing, head, and pronotum of this species (Deitz 1975a: figs. 38F, 40F, and 40R, respectively; redrawn here as Figs. 19–21). Our concept of *L. bituberculata* is based on these figures and the original description (Stål 1862e).

The specific name is a combination of the Latin terms "*bi*" (meaning "two") and "*tuberculata*" (meaning "tuberculate"), possibly referring to the prominent dorsal projections of the head.

Genus *Smerdalea* Fowler 1896e, **new tribal placement**

Smerdalea Fowler 1896e: 162. Type species: *Smerdalea horrescens* Fowler 1896e: 163, by monotypy.

Diagnosis.—The genus *Smerdalea* differs from other genera of Stegaspidini by having an elongate posterior pronotal process that terminates in a strongly dilated node with multiple spines. The forewing



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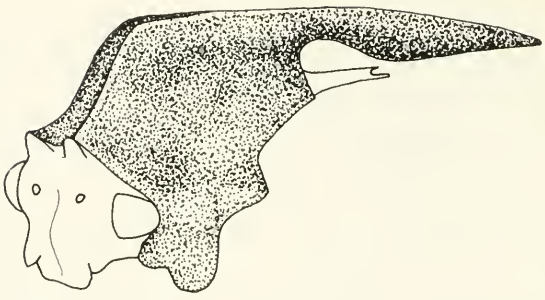

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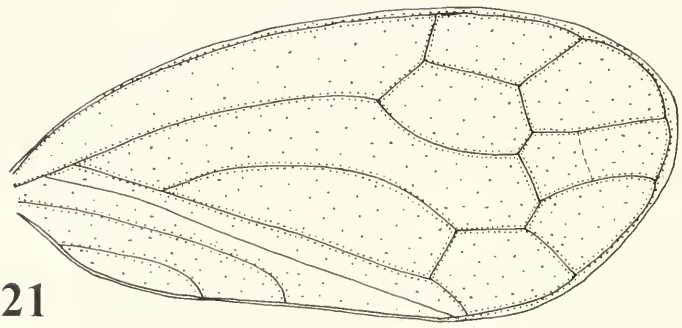

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Figs. 19–21. *Lirania bituberculata*, structures of the lectotype. 19, Head, anterior aspect (face). 20, Head, pronotum, and scutellum, anterolateral aspect. 21, Right forewing.

vein A_1 is partially confluent with the claval suture, and one r-m crossvein is present.

Adult.—*Dimensions* (mm): Total length 7.8–11.0. *Structure: Head:* Compound eyes elongate transversely, stalked or nearly so; ocelli on raised tubercles; dorsal projections distinct. *Thorax: Pronotum* (Fig. 24): Pronotum with humeral angles nearly acute; metopidium with distinct supraocular callosities; suprahumeral horns prominent; posterior pronotal process elongate, terminating with dilated node bearing multiple spines. *Pronotal surface sculpturing* (Fig. 30): Surface scabrous and punctate, each pit with one long, associated seta. *Scutellum* (Fig. 24): Elongate, usually dorsally produced at base, apex acuminate or emarginate. *Legs* (Fig. 25): Metathoracic femur with dorsal row of cucullate setae present; metathoracic tibia with 3 rows of enlarged, cucullate setae; metathoracic tarsomere I with apical cucullate seta. *Forewing* (Fig. 26): Coriaceous basally, with 1 r-m crossvein and vein A_1 partially confluent with claval suture. *Genitalia:* ♀: 2nd valvulae (Fig. 27) broadened abruptly at or past midlength, tapering distally, serrate dorsally; ♂ (Cryan and Deitz 1995a: fig. 6): styles hooked apically; aedeagus with anterior face of posterior arm denticulate preapically.

Range.—Peru[2]; Ecuador [USNM]; French Guiana [GMPC]; Panama[2]; Costa Rica [CNCI]; Guatemala[2]; Mexico [CNCI].

Material examined.—In addition to the specimens examined by Cryan and Deitz (1995a): 2 ♀ *S. horrescens* [CNCI].

Remarks.—Cryan and Deitz (1995a) recently revised the genus *Smerdalea*. Included in the present treatment of this genus is a description of one new species, a description of the previously unknown nymph of

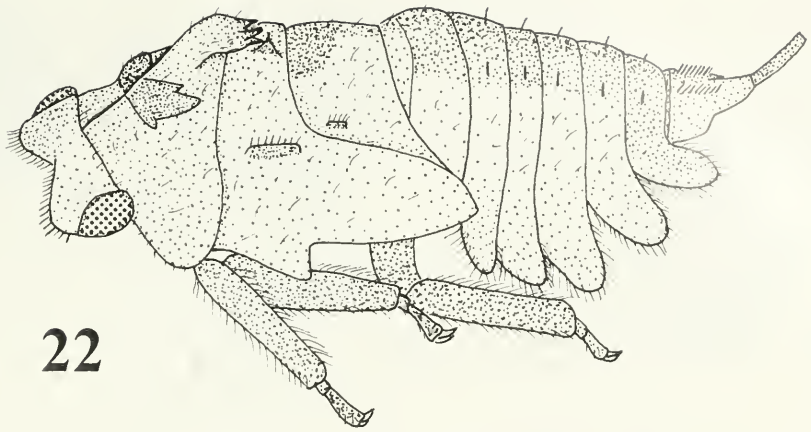


Fig. 22. *Smerdalea elevata*, late-instar nymph, anterolateral aspect.

S. elevata Cryan, and an updated key and a checklist to the species of *Smerdalea*.

KEY TO SPECIES OF *SMERDALEA*

1. Apex of scutellum emarginate 2
– Apex of scutellum acuminate 3
2. Pronotum with trifurcate suprahumeral horns (Fig. 24); basal node of posterior pronotal process with distinct tooth (Fig. 24) . . . . . *S. imminens* Cryan, new species
– Pronotum with suprahumeral horns culminating in a single process (Cryan and Deitz 1995a: fig. 9); basal node of posterior pronotal process lacking tooth (Cryan and Deitz 1995a: fig. 9) . . . . . *S. circumflexa* Cryan
3. Posterior pronotal process elevated high above scutellum (Cryan and Deitz 1995a: fig. 16); scutellum not produced subapically (Cryan and Deitz 1995a: fig. 16) . . . . . *S. elevata* Cryan
– Posterior pronotal process touching or nearly touching scutellum (Cryan and Deitz 1995a: fig. 2); scutellum produced subapically (Cryan and Deitz 1995a: fig. 2) . . *S. horrescens* Fowler

Smerdalea elevata Cryan (Fig. 22)

Late-instar nymph (Fig. 22).—Body dorsoventrally compressed; pronotum with stout precursors of suprahumeral horns and posterior process, in form resembling the adult but not elevated; mesonotum with lateral, comb-like row of bristles at base of each wing pad and paired dorsal chalazae; legs thin, not foliaceous; abdominal segments 4–8 with setose lateral lamellae and 1 stout seta on either side of dorsal midline; anal tube (abdominal segment 9) thin, slightly longer than other abdominal segments in dorsal view, with paired dorsal rows of stout setae at base.

Material examined.—1 nymph [USNM].

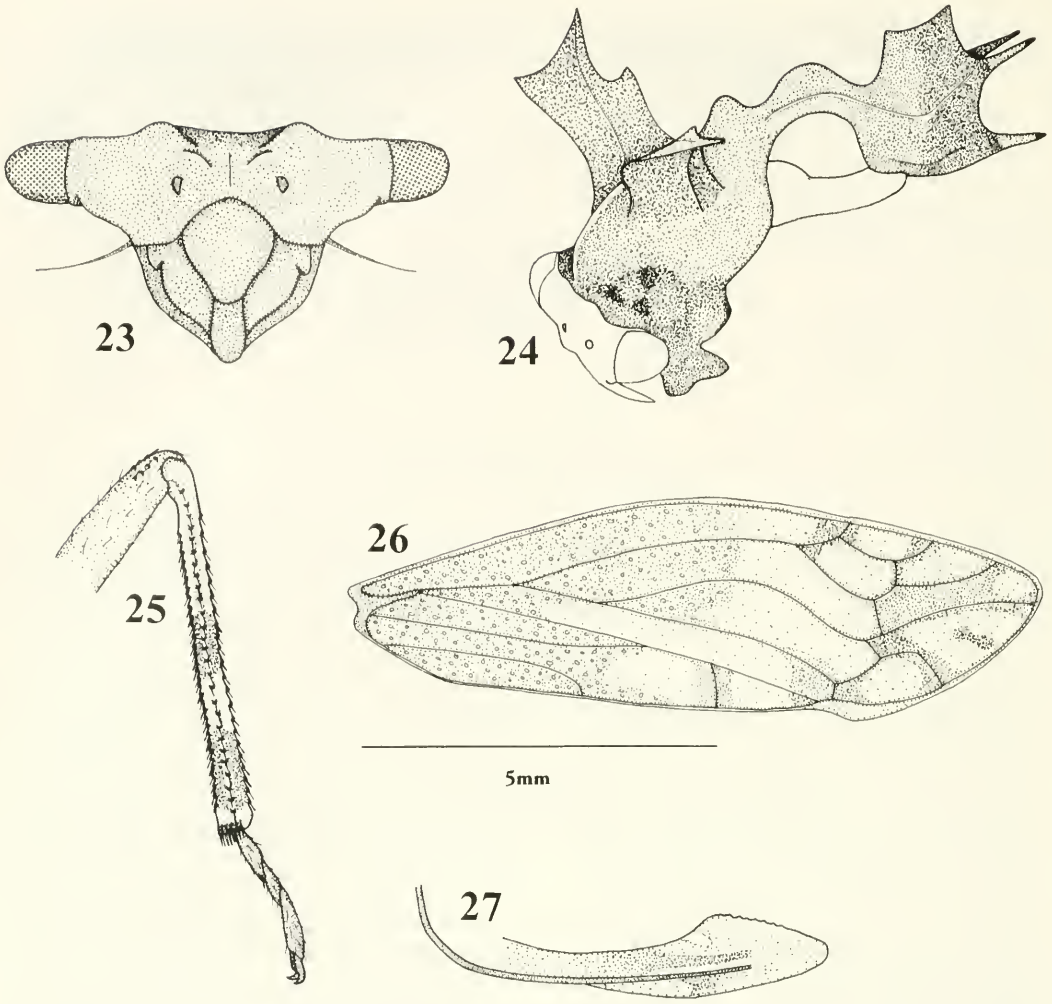
Remarks.—*Smerdalea elevata* was described from three females, all collected from the same forest plot (in the Río Tambopata Reserved Zone, Madre de Dios, Peru) by the Smithsonian Institution's Canopy Fogging Project. After the description was published, a single nymph was found in the same sample that yielded the adult type specimens. The posterior pronotal process of the nymph leaves no doubt as to its genus. Despite the fact that this nymph cannot be directly associated with the *S. elevata* adults, no other *Smerdalea* species are recorded from this locality. Thus, this specimen is thought to be the late-instar nymph of *S. elevata*.

***Smerdalea imminens* Cryan, new species** (Figs. 23–27)

Type locality.—Reserva Ethnica Waorani, Napo, Ecuador.

Diagnosis.—*Smerdalea imminens* has an emarginate scutellum and trifurcate suprahumeral horns.

Adult ♀.—*Dimensions* (mm): Total length 8.9–9.2; width between humeral angles 3.5–3.7; pronotal length 5.3–6.0; wing length 7.8–7.9; maximum width of head



Figs. 23–27. *Smerdalea imminens*, structures of the holotype. 23, Head, anterior aspect (face). 24, Head, pronotum, and scutellum, anterolateral aspect. 25, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 26, Right forewing. 27, Female second valvulae, lateral aspect.

across eyes 3.4–3.7. *Coloration:* Head and thorax mottled light and dark brown; apical node of posterior pronotal process dark brown with tan terminal spines tipped with black; legs light brown with dark brown transverse bands; forewings hyaline with dark brown maculae. *Structure: Head:* Face (Fig. 23) with fine pubescence; eyes stalked, transversely elongate; ocelli located just below centro-ocular line on low tubercles; dorsal projections distinct, separated by distance just greater than separation between ocelli, and bordering dorsal transverse ridge. *Thorax: Pronotum* (Fig. 24): Sparsely covered with fine, pale setae; metopidial sulcus depression with distinct supraocular callosities; humeral angles produced, nearly acute; suprahumeral horns smoothly edged (not serrate), rising obliquely away from body (in anterior aspect), trifurcate at about ⅔ length with central process largest; dorsal transverse ridge evident from each central process to base of suprahumeral horn; posterior pronotal process arched, with basal and apical nodes; basal node unadorned; apical node laterally

compressed, with one stout dorsal spine and three posterior spines of subequal length; apical node rests in scutellar emargination. *Scutellum* (Fig. 24): Elongate, elevated anteriorly, then flattened; apex emarginate and slightly raised to meet apical node of posterior pronotal process. *Legs* (Fig. 25): Metathoracic femur with dorsal row of 7–12 cucullate setae; metathoracic tibia with enlarged setal rows I, II, and III distinct, each bearing cucullate setae (22–26, 25–29, and 30–34, respectively); area between setal rows I and II slightly sulcate. *Forewing* (Fig. 26): Basal ⅓ coriaceous (except area between claval suture and Cu). *Genitalia:* 2nd valvulae (Fig. 27) abruptly broadened at about ⅔ of its length, remaining broadened to apex; dorsal ridge of broadened apical ⅓ with distinct serrations. ♂: Unknown.

Late-instar nymph.—Unknown.

Distribution.—Ecuador [USNM]; French Guiana [GMPC].

Material examined.—Holotype [♀, dissected] [USNM] with labels: "MEMB 172/LOT #870," "ECUADOR: NAPO Res. Ethnica/Waorani, 1 km S. Onkone Gare/Camp, Trans.Ent. 6 Oct. 1994/220 m 00°39′10″ S 076°26′W/T. L. Erwin et. al," "Insecticidal fogging of mostly bare/green leaves, some with covering/of lichenous or bryophytic plants in/terre firme forest At trans 9,/Sta. 1 Project MAXUS Lot870," and "HOLOTYPE/*Smerdalea/imminens*/J. R. Cryan." Paratype [♀] [GMPC] deposited in MNHN, with labels: "GUYANE (Régina)/Montagne de Kaw/PK36 22.IX.93/G. MORAGUES," "piège lumineux," and "PARATYPE/*Smerdalea/imminens*/J. R. Cryan."

Remarks.—*Smerdalea imminens* is closely related to *S. circumflexa* Cryan, as evidenced by the emargination of the scutellum. These species differ principally in the nature of the suprahumeral horns (*S. circumflexa* has unbranched suprahumeral horns) and in the shape of the female ovipositor (the 2nd valvulae of *S. imminens* and *S. circumflexa* have the same general shape, although the 2nd valvulae of the former is narrower).

The specific name is from the Latin "immineo" (to threaten), referring to the threatening, dangerous appearance of this species.

Species Checklist of *Smerdalea*

circumflexa Cryan

Smerdalea circumflexa Cryan, in Cryan and Deitz 1995a: 9.

elevata Cryan

Smerdalea elevata Cryan, in Cryan and Deitz 1995a: 10.

horrescens Fowler

Smerdalea horrescens Fowler 1896e: 163.

imminens Cryan, **new species**

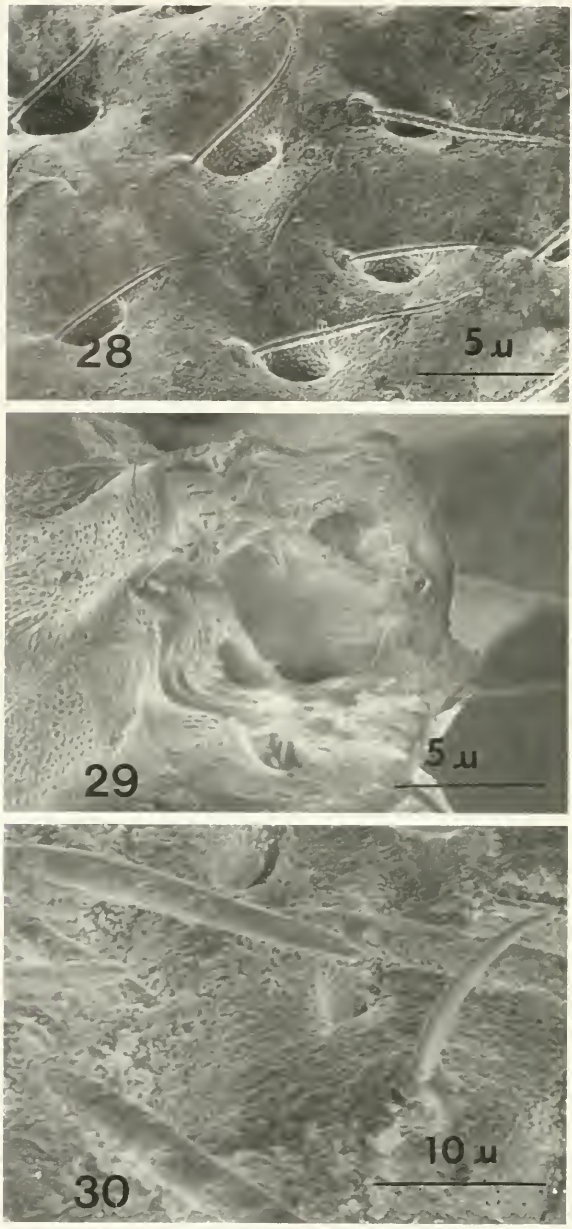
Smerdalea imminens Cryan, new species

Summary

Recent taxonomic changes in the tribe Stegaspidini are summarized in Table 1. Currently, two stegaspidine genera are monotypic: *Flexocentrus* (*F. felinus,* for which both sexes are known) and *Lirania* (*L. bituberculata,* known only from a female specimen). Immature stages are unknown for all species of the genera *Lirania, Oeda, Stylocentrus,* and *Umbelligerus.*

Biogeographically, the tribe Stegaspidini is most diverse in the mid-latitudes of South America. The distribution of the nine stegaspidine genera is as follows: Mexico (2 genera), Guatemala (2), Honduras (2), Nicaragua (1), Costa Rica (6), Panama (5), Colombia (5), Trinidad (3), Venezuela (7), Guyana (7), Suriname (5), French Guiana (7), Ecuador (7), Peru (7), Brazil (8), Bolivia (5), Paraguay (2), and Argentina (2).

Information regarding stegaspidine host plants needs to be increased. Reliable host records are available for only a few species in the genera *Bocydium, Flexocentrus, Lycoderes, Oeda,* and *Stylocentrus.* To date, records for these genera are from the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae. In addition,



Figs. 28–30. Pronotal metopidium surface sculpturing of Stegaspidini. 28, *Bocydium globulare*. 29, *B. duoglobum*. 30, *Smerdalea elevata*.

questions regarding voltinism, degree of presociality, and forces behind the development and evolution of the often-bizarre pronotal shapes of these insects remain unanswered.

Stegaspidini is the nominate tribe of Stegaspidinae, one of the more plesiomorphic membracid subfamilies (Dietrich and Deitz 1993a). Certain morphological characters appear more derived in Stegaspidini than in its sister tribe, Microcentrini; the evolutionary relationships among the tribes and genera of Stegaspidinae will be explored in a phylogenetic analysis of the subfamily (Cryan and Deitz, in preparation).

Table 1. Summary of taxonomic changes in Stegaspidini Haupt.

Deitz 1975a[1]	*Cryan and Deitz (present)*
Subfamily Stegaspidinae[2] Haupt	Subfamily Stegaspidinae Haupt
Tribe Stegaspidini[3] Haupt	Tribe Stegaspidini Haupt
Bocydium Latreille (9 spp.)	*Bocydium* Latreille (15 spp.)
Stylocentrus Stål (3 spp.)	*Stylocentrus* Stål (3 spp.)[4]
Umbelligerus, New Genus (1 sp.)	*Umbelligerus* Deitz (3 spp.)[4]
Oeda Amyot and Serville (4 spp.)	*Oeda* Amyot and Serville (4 spp.)[4]
Lycoderes Germar (22 spp.)	*Lycoderes* Germar (36 spp.)[4]
Stegaspis Germar (10 spp.)	*Stegaspis* Germar (2 spp.)[4]
Flexocentrus Goding (2 spp.)	*Flexocentrus* Goding (1 sp.)[4]
Lirania Stål (1 sp.)	*Lirania* Stål (1 sp.)
	Smerdalea Fowler (4 spp.)
Euwalkeria Goding (1 sp.)	(*Euwalkeria* removed from Stegaspidini by Deitz and Dietrich [1993a])

[1] Species counts based on Metcalf and Wade (1965a).
[2] As Stegaspinae.
[3] As Stegaspini.
[4] Discussed in Cryan and Deitz (in preparation).

Finally, independent phylogenetic analyses of morphological characters (Cryan and Deitz, in preparation; Dietrich et al., in preparation) and DNA nucleotide sequence data (Cryan and Wiegmann, in preparation) indicate that the genus *Deiroderes* Ramos is included in the subfamily Stegaspidinae. The tribal affiliation of *Deiroderes,* however, is unclear, and may even warrant a new tribe within the subfamily. Cryan and Deitz (in preparation) will present a revision of *Deiroderes* based on morphology.

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PLATYSCYTISCA BERGMANNAE, A NEW GENUS AND SPECIES OF NEOTROPICAL PLANT BUG RESEMBLING SPECIES OF *PLATYSCYTUS* REUTER (HETEROPTERA: MIRIDAE: PHYLINAE)

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Abstract.—The new genus ***Platyscytisca*** is described to accommodate the new species ***P. bergmannae***, collected in São Paulo, Brazil, on *Ficus* sp. A dorsal and ventral habitus, male genitalia, male genital capsule, and male and female antennae are illustrated to help with recognition. *Amazonophilus* Carvalho and Costa is resurrected from synonymy under *Platyscytus* Reuter, and its relationship to *Platyscytisca* is discussed.

Key Words: Insecta, Heteroptera, Miridae, Phylinae, *Platyscytisca,* new genus, *bergmannae,* new species, Brazil

During cooperative work on New World Miridae, we discovered a peculiar new phyline that was taken on *Ficus* sp. in São Paulo, Brazil. Externally, this new species resembles some taxa now included in the Neotropical genus *Platyscytus* Reuter (Carvalho 1958, Carvalho and Costa 1994, Schuh 1995) or *Amazonophilus* (Carvalho and Costa 1993), a genus recently synonymized by Kerzhner and Schuh (1995).

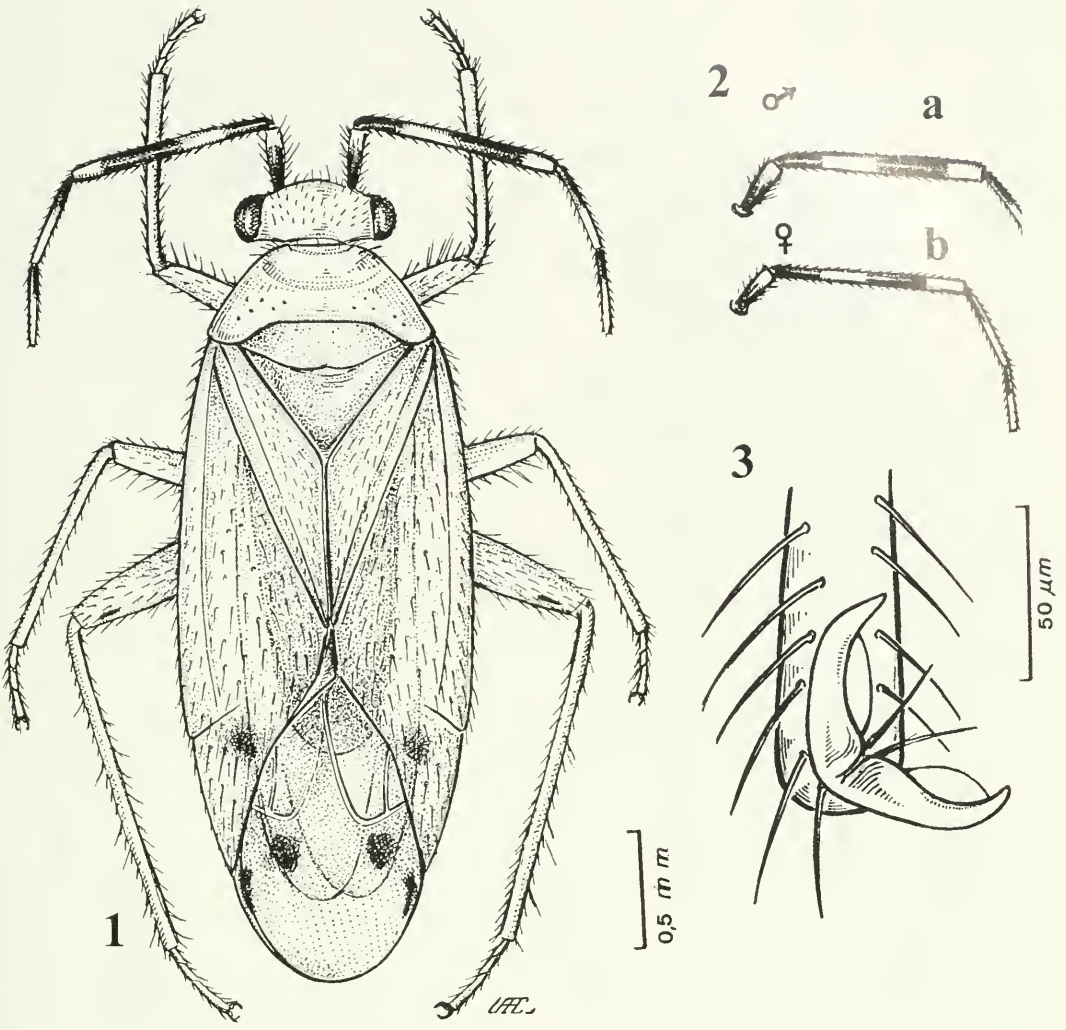
Herein, we describe the new genus *Platyscytisca* to accommodate the new species *Platyscytisca bergmannae* and provide a dorsal and ventral habitus and illustrations of the pretarsus, male genitalia, male genital capsule, and male and female antennae. *Amazonophilus* is resurrected from synonymy under *Platyscytus,* and the relationship to *Platyscytisca* is discussed.

Platyscytisca Costa and Henry, new genus

Type species.—*Platyscytisca bergmannae,* new species.

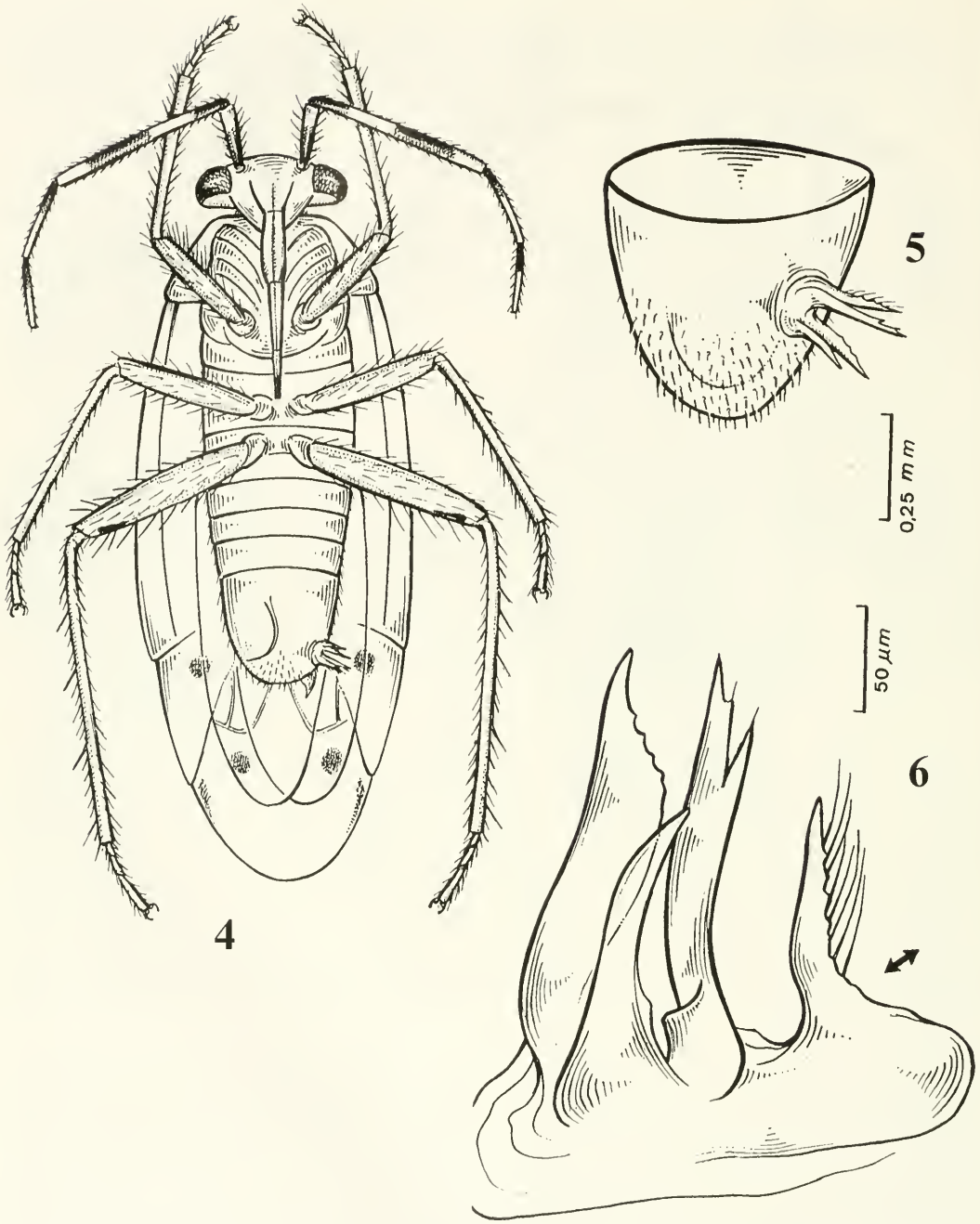
Diagnosis.—This new genus is distinguished from other phyline mirids by the combination of the overall pale coloration, banded second antennal segment, broad head with the concave vertex, pale hemelytra with a small, round, dark spot on the cuneus and another on the membrane just distal to the large areole, cluster of four spines on the male genital capsule, and by the long, slender vesica, with a very slender, sharply bent, apical process.

Description.—Small, delicate phyline, overall coloration pale or whitish. Head impunctate, much broader than long, convex anteriorly in dorsal aspect, strongly produced ventrally below eyes a distance slightly greater than the lateral height of an eye, vertex wide, concave, wider than combined dorsal widths of eyes. Rostrum slender, extending to metacoxae or beyond. Antenna relatively slender; segments I and II subequal in diameter; segments III and IV more slender; segment II longest, with two



Figs. 1–3. *Playtscytisca bergmannae*. 1, Dorsal adult habitus. 2, Antenna (a, male; b, female). 3, Pretarsal claw.

dark bands. Pronotum impunctate, much wider than long, posterior width wider than anterior width, lateral margins rounded, basal margin distinctly emarginate; calli weakly delimited laterally and posteriorly by a shallow impressed line. Mesoscutum distinctly swollen transversely and raised well above surface of pronotum; scutellum subequilateral, slightly wider than long, middle of base raised to level of mesoscutum, then gradually sloping to level of hemelytra. Hemelytron impunctate, translucent; cuneus longer than wide with a small dark spot on basal half; membrane translucent, with two areoles and a small dark spot just beyond large areole and a slender fuscous streak near apex of cuneus. Ventral surface pallid. Legs slender, unmarked; tibial spines slender, pale; claws typically phyline, arolia large, fleshy, extending nearly to apex of each claw. Genital capsule typically rounded, with a cluster or field of four spines (Figs. 4–6) ventrolaterally on left side, two lateral spines shorter and two, sometimes branched, inner ones longer. Vesica (Fig. 7a) long and slender, apical third more slen-



Figs. 4–6. *Platyscytisca bergmannae*. 4, Ventral adult habitus. 5, Male genital capsule showing position of spine cluster. 6, Cluster of spines on male genital capsule enlarged.

der, sharply bent, apex with an even more slender, sharply bent, weakly serrated process (Fig. 7b); left paramere (Figs. 8a, b) with a distinct crescent-shaped lateral process having ventral arm of crescent bifid; right paramere simple, rounded (Fig. 9); phallotheca (Fig. 10).

Etymology.—*Platyscytisca* is a noun de-

rived from the generic name *Platyscytus* and the suffix "isca," taken from the Anglo Saxon "isc," denoting "origin or pertaining to," to draw attention to the overall similarity of it to *Platyscytus*. The gender is feminine.

Remarks.—*Platyscytisca* appears similar to *Amazonophilus* Carvalho and Costa and some species of *Platyscytus* Reuter based on the structure of the head, overall pale coloration, banded antennae, and dark spots on the cuneus and membrane, but very different genitalia suggest that this resemblance simply reflects convergence. The peculiar vesica having a slender, abruptly narrowed apical process, the cluster of four distinct, apically acute spines on the left lateroventral area of the male genital capsule, and the crescent-shaped lateral process on the left paramere appear quite unique in the Neotropical mirid fauna.

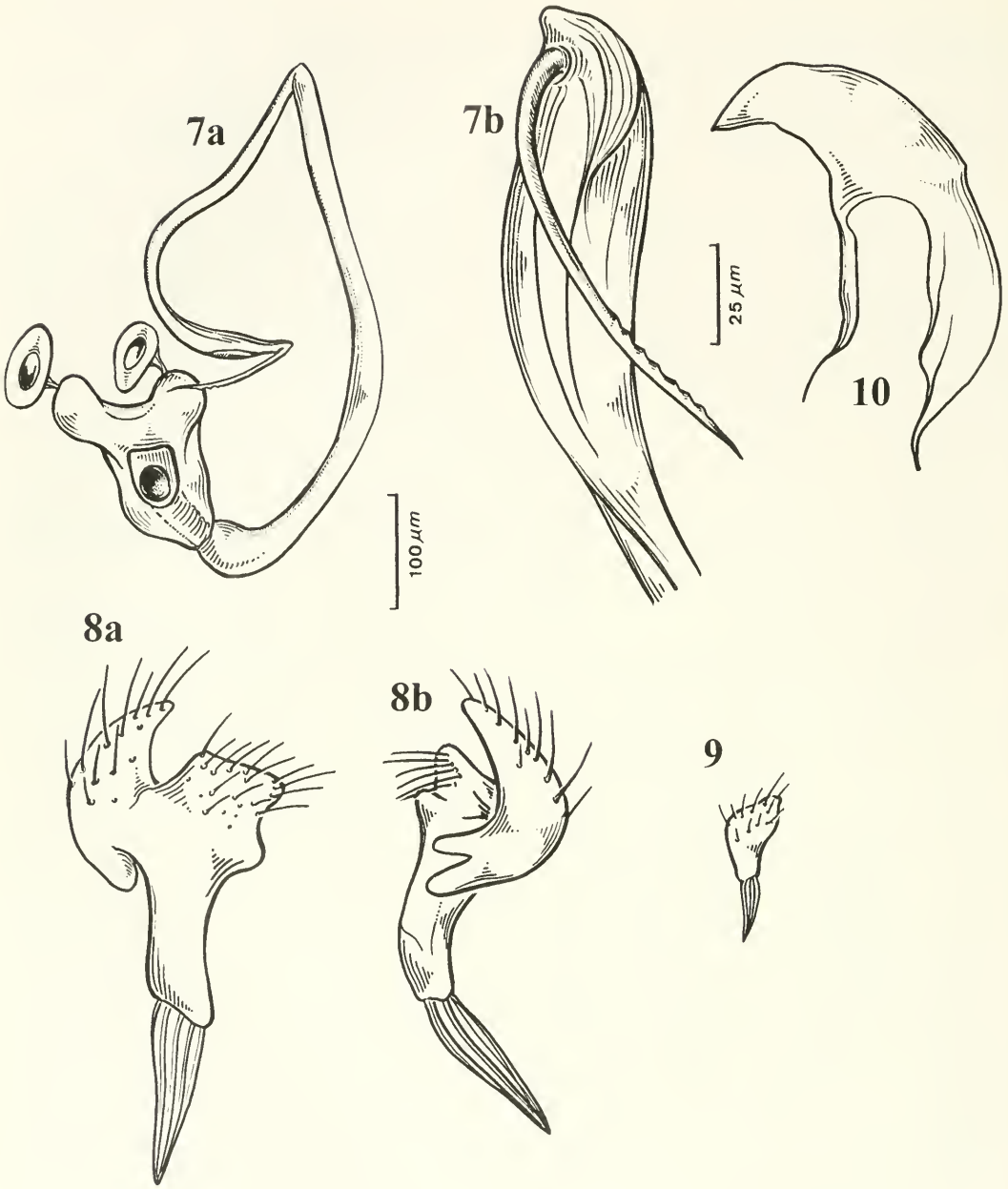
We note that Kerzhner and Schuh (1995) synonymized *Amazonophilus* under *Playtscytus* by stating "Judging from the habitus figure and illustrations of male genitalia, *bipunctatus* is a species of *Playtscytus,* and we are so treating it." Although we have not studied the genitalia of the type of the genus, *P. binotatus* Reuter (nor have the genitalia been illustrated in the literature), we have examined the similar *P. blantoni* Carvalho (1955), and find that the extremely long, nearly filamentous vesica of *Amazonophilus bipunctatus* Carvalho and Costa, having multiple coils, is quite unlike the relatively short, stout vesica of *P. blantoni*, having only a single coil. In addition, Carvalho (1955) considered the short, singly coiled vesica of *P. tucumanus* (Carvalho 1953) of the same generic type as *P. binotatus*. Our observations also indicate that *Platyscytus* is likely not monophyletic and seems to be made up of at least three species groups, each of which probably represents a separate genus. Based on this information, we feel it is premature to consider *Amazonophilus* a junior synonym of *Platyscytus* and, therefore, resurrect *Amazonophilus,* **revised status,** recognizing that much more work on these seemingly similar taxa is needed.

Platyscytisca bergmannae Costa and Henry, new species

(Figs. 1–10)

Diagnosis.—*Platyscytisca bergmannae* is best distinguished by the generic characters, particularly by the cluster of four spines on the male genital capsule and the structure of the left paramere and vesica. The combination of a dark first antennal segment, two bands on the second antennal segment, and the small round dark spot on each cuneus and one on the membrane just beyond the large areole (and a narrow fuscous streak just beyond apex of cuneus) will distinguish this species from similar appearing species of *Platyscytus*.

Description.—*Male* (n = 5): Length 2.80–3.04 mm, width 0.98–1.16 mm. *Head:* Dorsal length 0.30–0.32 mm, width 0.62–0.66 mm, vertex 0.32–0.34 mm; uniformly pale or whitish. *Rostrum:* Length 0.80–0.84 mm, extending to about metacoxae. *Antenna* (Figs. 2a, b): Segment I, length 0.24 mm, dark brown to fuscous, paler at apex; II, 0.88–1.00 mm, pale or whitish, with basal ¼ and a broad band on apical ½ fuscous; III, 0.30–0.34 mm, pale or white, with basal ½ fuscous; IV, 0.30–0.32 mm, pale or white, with basal ⅓ fuscous. *Pronotum:* Length 0.34–0.36 mm; basal width 0.86–0.92 mm; uniformly pale or whitish. *Hemelytron:* Uniformly pale or whitish, large portion of clavus, corium, and membrane translucent; a small fuscous spot on basal ½ of cuneus, and on membrane a round fuscous spot just distal to large areole and a fuscous streak just beyond apex of cuneus. *Ventral surface:* Uniformly pale or whitish. *Legs:* Uniformly pale or whitish; tibial spines small, pale; claws with large fleshy arolia (Fig. 3). *Male genitalia:* Genital capsule evenly rounded, with field of four prominent spines (Figs. 5, 6); vesica (Figs. 7a, b); left paramere (Figs. 8a, b); right paramere (Fig. 9); phallotheca (Fig.10).



Figs. 7–10. *Platyscytisca bergmannae*. 7, Vesica (a, entire structure, including phallobase; b, Apex showing slender apical process). 8, Left paramere (a, lateral aspect; b, lateral aspect, rotated 180° from Fig. 8a). 9, Right paramere. 10, Phallotheca.

Female (n = 7): Length 2.72–0.288 mm, width 1.12–1.14 mm. *Head:* Length 0.32–0.34 mm, width 0.64–0.66 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 0.82–0.86 mm. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.78–0.84 mm; III, 0.34–0.36 mm; IV, 0.26–0.30 mm. *Pronotum:* Length 0.34–0.36 mm, basal width 0.84–0.92 mm.

Etymology.—This species is named in honor of its collector, Dr. Eliana Cherubini

Bergmann (Instituto Biológico, São Paulo, Brazil).

Type specimens.—Holotype ♂, Brasil, S. P., São Paulo, Instituto Biológico, May 1997, E. C. Bergmann coll., taken on *Ficus* sp. (Museu Nacional, Rio de Janeiro, Brasil). Paratypes: 16 ♂, 32 ♀, May 1997 & 19 March 1998, same locality and collector as for holotype (Museu Nacional; National Museum of Natural History, Smithsonian Institution, Washington, DC, USA).

Remarks.—All specimens have been in alcohol, so the quality of many is poor.

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A NEW SPECIES OF *DASYHELEA* KIEFFER (DIPTERA: CERATOPOGONIDAE) AND NEW RECORDS OF BITING MIDGES FROM THE STATE OF SAN LUIS POTOSI, MEXICO

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Abstract.—Four previously described species of Ceratopogonidae: *Lasiohelea anitae* (Huerta and Ibáñez-Bernal), *Forcipomyia* (*Thyridomyia*) *nodosa* Saunders, *Dasyhelea scissurae* Macfie, and *Culicoides* (*Haematomyidium*) *paraensis* (Goeldi), are recorded for the first time in the State of San Luis Potosi, Mexico. In addition, descriptions and illustrations of ***Dasyhelea huasteca,* new species,** and the female of *Lasiohelea anitae* (Huerta and Ibáñez-Bernal) are presented.

Resumen.—Se registran por primera vez para el estado de San Luis Potosí, México, cuatro especies de Ceratopogonidae previamente descritas: *Lasiohelea anitae* (Huerta e Ibáñez-Bernal), *Forcipomyia* (*Thyridomyia*) *nodosa* Saunders, *Dasyhelea scissurae* Macfie y *Culicoides* (*Haematomyidium*) *paraensis* (Goeldi). Adicionalmente, se presentan las descripciones e ilustraciones de ***Dasyhelea huasteca* nueva especie** y de la hembra de *Lasiohelea anitae* (Huerta e Ibáñez-Bernal).

Key Words: Diptera, Ceratopogonidae, *Lasiohelea, Forcipomyia, Dasyhelea, Culicoides,* Mexico, San Luis Potosi, new species

The Ceratopogonidae remain poorly studied in many areas of Mexico, for example, the Mexican Plateau is a region of current interest for faunistic studies. Some states in this area, such as the states of Mexico and Aguascalientes, have no ceratopogonid species recorded at present. Near these states is San Luis Potosi, with nine species of biting midges previously recorded: *Forcipomyia incubans* (Macfie), *F. mexicana* Wirth, *Culicoides blantoni* Vargas and Wirth, *C. eadsi* Wirth and Blanton, *C. neopulicaris* Wirth, *Stilobezzia coquilletti* Kieffer, *Paryphoconus anomalicornis* Kieffer, *P. maya* Spinelli and Wirth, and *Stenoxenus johnsoni* Coquillett.

We recently studied some specimens of *Lasiohelea* Kieffer, *Forcipomyia* Meigen, *Dasyhelea* Kieffer, and *Culicoides* Latreille, collected near the towns of San Antonio and San Martin Totolteo in San Luis Potosi, and found new geographical records of four species, as well as the an undescribed species of *Dasyhelea* and the previously unknown female of *Lasiohelea anitae* (Huerta and Ibáñez-Bernal).

We follow Yu and Wirth (1997) and consider *Lasiohelea* as a genus instead of a subgenus of *Forcipomyia.* We used the slide mounting method suggested by Borkent and Bissett (1990), and the morphological terms of Downes and Wirth (1981). All the specimens are deposited in the Collection of Arthropods with Medical Impor-

tance of the Instituto Nacional de Diagnostico y Referencia Epidemiologicos (INDRE), Secretaria de Salud, Mexico.

Lasiohelea anitae (Huerta and Ibáñez-Bernal)
(Figs. 1–8)

Forcipomyia (Lasiohelea) anitae Huerta and Ibáñez-Bernal 1996: 350, figs. (♂, Mexico, Chiapas).

Female description.—*Head:* Eyes bare, mesally with ocular margins in contact, but with marginal facets separated at narrowest distance by one to one and a half facet diameters (Fig. 3). Flagellum brown (Fig. 1); lengths of flagellomeres (μm): 30-20-22-22-22-23-24-27-63-68-69-70-98; antennal ratio (AR): 1.76 (1.70–1.82; n = 3); basal flagellomeres semispherical, flagellomere 8 with 6–7 basiconica sensilla. Palpus (Fig. 2) with lengths of segments (μm): 0.3-42-22-35; palpal ratio (PR): 1.1 (1.0–1.3, n = 3); third segment swollen at midlength, with a large oval pit, containing several small, irregularly arranged sensilla capitata. Mandible (Fig. 4) with 30–32 small teeth; mandible length (μm): 108.5, width (μm): 17.6. Cibarial armature with 15 or 16 teeth in single row (Fig. 5); each tooth with basal apodeme, each about double tooth length.

Thorax: Scutum, scutellum brown; legs uniformly pale yellowish. Tarsal ratios of foreleg (I), midleg (II), hindleg (III) (TR): I: 2.38 (2.36–2.42), II: 2.0 (2.0), III: 2.0 (2.0–2.1) (n = 3); hind tibial comb with 7 spines, one near spur longest. Wing (Fig. 6) with radial cells coalesced, slitlike; wing length: 0.83 mm (0.82–0.85; n = 3), width: 0.34 mm (0.32–0.35; n = 3), costal ratio (CR): 0.59 (0.59–0.60; n = 3). Halter pale.

Abdomen: Brown. Genitalia (Fig. 8) with 3 small lobes arising at different level from posterior base of genital fork; spermatheca (Fig. 7) partially collapsed in examined material.

Distribution.—Mexico (Chiapas, San Luis Potosi).

Specimens examined.—3 ♀, 1 ♂. Mexico: San Luis Potosi, San Antonio, El Puente, April 23, 1997, Malaise trap, Paz-Rodríguez, R. & Pérez-Rentería, C., cols.

Comments.—The female of this species can be associated with the male by the number and arrangement of the cibarial teeth, the form of the palpus and the frontal sclerite, the body coloration, and the arrangement and form of the sensilla on the flagellomeres. The single male collected from San Luis Potosi was compared with the type specimens previously described by Huerta and Ibáñez-Bernal (1996).

Unfortunately, the descriptions of females of most American species of *Lasiohelea* do not include many important characteristics useful for their separation, such as the number of cibarial and mandibular teeth, and certain ratios, thereby making species determination very difficult. We believe it is necessary to redescribe most of the American species in order to recognize the important characteristics useful for separating these species (Yu and Wirth 1997).

Forcipomyia (Thyridomyia) nodosa Saunders
(Fig. 9)

Forcipomyia (Thyridomyia) nodosa Saunders 1959: 43 (all stages, Costa Rica, figs.).

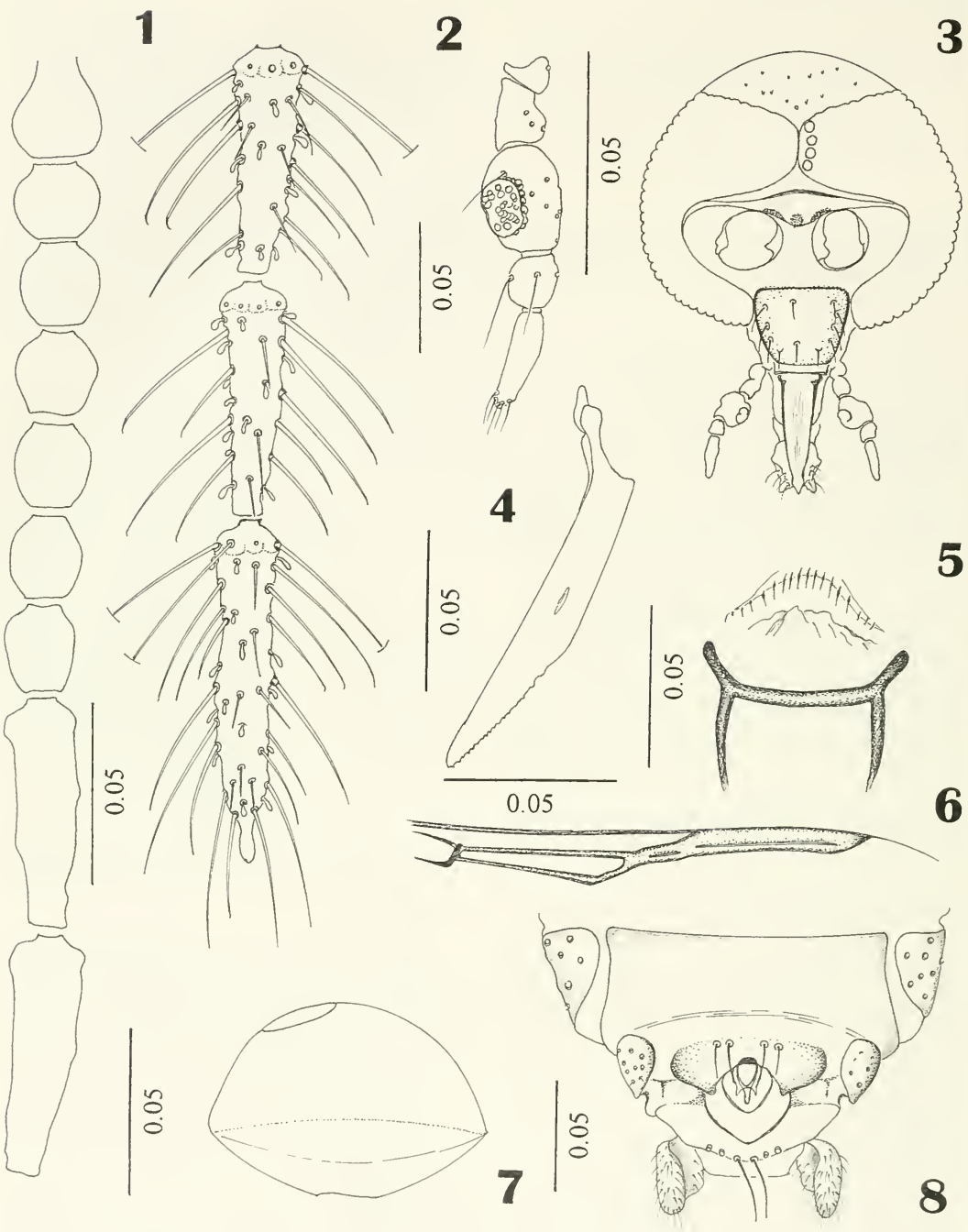
Several specimens of this species were collected in San Luis Potosi. An illustration of the male genitalia is presented in Fig. 9. Dow and Wirth (1972) gave detailed redescriptions of both sexes.

Distribution.—U.S.A.; Mexico (Baja California, Sonora, Sinaloa, San Luis Potosi); Costa Rica; Colombia.

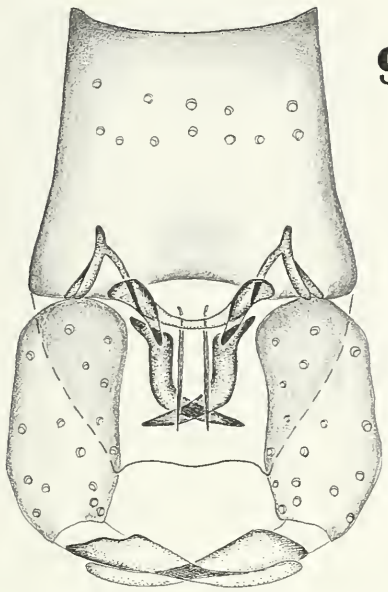
Specimens examined.—8 ♂, 6 ♀. Mexico: San Luis Potosi, San Antonio, El Puente, April 23, 1997, Malaise trap, Paz-Rodríguez, R. & Pérez-Rentería, C., cols.

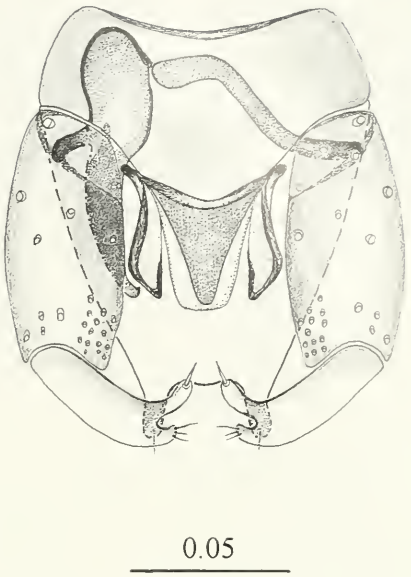
Dasyhelea scissurae Macfie
(Fig. 10)

Dasyhelea scissurae Macfie 1937: 15 (♂, Trinidad, figs.).



Figs. 1–8. *Lasiohelea anitae*, female. 1, Flagellomeres. 2, Palpus. 3, Head. 4, Mandible. 5, Cibarial armature. 6, Anterior veins of wing. 7, Spermatheca. 8, Abdomen, distal segments, in ventral view. Scale lines in millimeters.





Figs. 9–10. Male genitalia, in ventral view. 9, *Forcipomyia (Thyridomyia) nodosa.* 10, *Dasyhelea scissurae.* Scale line in millimeters.

This is the first record of this species from the state of San Luis Potosi, and only the second record from Mexico (Ibáñez-Bernal et al. 1996). We provide an illustration of the male genitalia (Fig. 10).

Distribution.—Mexico (San Luis Potosi, Guerrero); Costa Rica; Bermuda; Trinidad; Argentina.

Specimens examined.—17 ♂, 11 ♀. Mexico: San Luis Potosi, San Martin Totolteo, April 24, 1997, Malaise trap, Paz-Rodríguez, R., Pérez-Rentería, C., cols. Seven males mounted on slides; the remaining specimens preserved in ethanol.

Dasyhelea huasteca Huerta and Ibáñez-Bernal, new species

(Figs. 11–16)

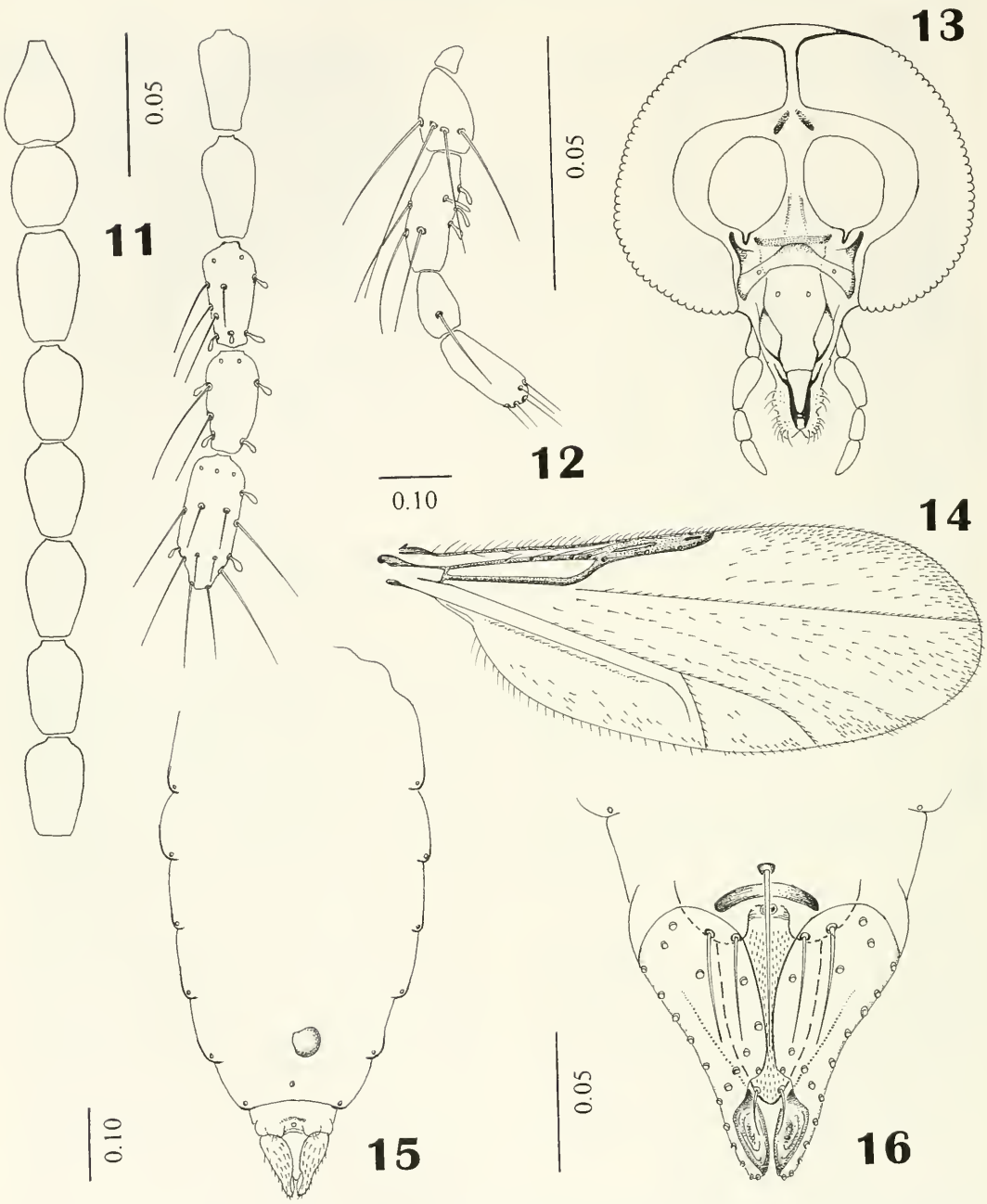
Diagnosis.—Small brown species, with the fifth tarsomeres dark and female cerci spatula-like.

Female.—*Head* (Fig. 13): Dark brown. Eyes with short pubescence, separated at narrowest distance by 5 μm. Frontal sclerite with two small, inclined, sclerotized bars. Flagellum (Fig. 11) brown; antennal ratio (AR): 0.72; with more or less cylindrical non-reticulate flagellomeres, with lengths (μm): 37-30-30-32-32-35-35-35-35-35-37-37-46. Palpus (Fig. 12) yellowish; lengths of segments (μm): 27-42-22-35; palpal ratio (PR): 2.2; third segment with a few sensilla capitata on mid portion of mesal surface.

Thorax: Scutum and postscutellum dark brown; scutellum yellowish. Legs pale yellowish, apex of femora, base of tibia darkish, fifth tarsomeres dark; hind tibial comb with four spines, one nearest spur, short; hind tarsal ratio 1.9. Wing (Fig. 14) length: 0.74 mm; width: 0.31 mm. Wing membrane with macrotrichia extending from near base of vein r-m to wing margin; cell r_1 narrow, nearly twice length of cell r_2 closed; vein r-m oblique. Costal ratio (CR): 0.50. Halter with brown stem, white knob.

Abdomen (Fig. 15): Brown. Genitalia (Fig. 16) lightly sclerotized arched subgenital plate; cerci very long, with spatula-like cover on mesal sides of ventral surfaces, cercus length 98.4 μm. Spermatheca subspherical (Fig. 15) measuring 0.04 mm by 0.031 mm, and a second rudimentary spermatheca present. Spermathecal/cercus length: 0.44.

Male.—Unknown.



Figs. 11–16. *Dasyhelea huasteca*, female. 11, Flagellomeres. 12, Palpus. 13, Head. 14, Wing. 15, Abdomen showing the two spermathecae, in ventral view. 16, Abdomen, distal segments, in ventral view. Scale lines in millimeters.

Types.—Holotype ♀, 1 ♀ Paratype: San Antonio, El Puente, April 23, 1997, Malaise Trap, Paz-Rodríguez, R., and Pérez-Rentería, C., cols. Both specimens deposited in the Collection of Arthropods with Medical Importance of the Instituto Nacional of Diagnostico and Referencia Epidemiologicos (INDRE).

Etymology.—The name *huasteca* refers to the natural region of Mexico that extends from the maritime slope of the Sierra Madre Oriental to the Gulf of Mexico, between the river Cazones and the Tamesi basin. The region includes the southern part of the state of Tamaulipas, the northern area of the state of Veracruz, the oriental strip of the state of San Luis Potosi, in which the specimens were collected, and a small sector of the states of Puebla and Hidalgo. The region was inhabited in the past by the *huastecas,* a pre-Columbian Mexican people of the Maya-quiche group, now restricted to two small areas inside the region.

Comments.—Only two species of *Dasyhelea* have modified spatula-like cerci: *D. spathicerca* Wirth and *D. huasteca.* However, *D. spathicerca* differs from this new species because it has the two well developed spermathecae, wing is larger (wing length 1.11 mm), has a greater antennal ratio (0.68), the cerci are thinner and shorter, and the ratio of spermathecal length/cercus length is only 0.36.

It is very difficult to place this species in the subgenera proposed by Remm (1962, 1979) or in the species-groups proposed by Wirth (1952) and Waugh and Wirth (1976) because of the considerably modified female cerci and subgenital plate. The flagellomeres are more or less similar to other species in the *Leptobranchia* group of Waugh and Wirth (1976), but the third segment is shorter than the combination of fourth and fifth palpal segments. Therefore, we can not accurately place *D. huasteca* in any of the species-groups or subgenera proposed to date, and its true affinities are unknown.

Culicoides (Haematomyidium) eadsi Wirth and Blanton

Culicoides eadsi Wirth and Blanton 1971: 37 (♂, ♀, Texas).

This species was previously reported for this region by Wirth and Blanton (1971).

Distribution.—U.S.A. (Texas, Florida); Mexico (Sonora, Nayarit, San Luis Potosi, Yucatan); Cuba.

Specimens examined.—1 ♀. Mexico, San Luis Potosi, San Antonio, El Puente, April 23, 1997, Malaise trap, Paz-Rodríguez, R., Pérez-Rentería, C., cols.

Culicoides (Haematomyidium) paraensis (Goeldi)

Haematomyidium paraensis Goeldi 1905: 137 (♀, Brazil).

Culicoides undecimpunctatus Kieffer 1917: 307 (♀, Argentina).

This is the first record of this species from the state of San Luis Potosi.

Distribution.—Eastern U.S.A.; Mexico; Central and South America south to Argentina; Barbados, Grenada and Trinidad in the West Indies.

Specimen examined.—1 ♀. Mexico, San Luis Potosi, San Antonio, El Puente, April 23, 1997, Malaise trap, Paz-Rodríguez, R., Pérez-Rentería, C., cols.

Acknowledgments

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WHAT IS THE REAL *ISWAROIDES* (HYMENOPTERA: TIPHIIDAE: THYNNINAE)?

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Abstract.—Phylogenetic relationships among *Iswaroides* Ashmead, *Thynnoturneria* Rohwer, *Acanthothynnus* Turner, *Aspidothynnus* Turner, and *Epactiothynnus* Turner are reexamined. As a result of this analysis, synonymy of *Thynnoturneria* under *Iswaroides* is confirmed. *Iswaroides* is redescribed and species placements corrected for this revised generic grouping. Twenty-three species are placed in *Iswaroides,* and the new species ***Iswaroides robusta*** is described.

Key Words: Tiphiidae, Hymenoptera, *Iswaroides, Thynnoturneria,* Australia, *Acanthothynnus, Aspidothynnus, Epactiothynnus*

Several generic groupings of Australian thynnine tiphiids are part of the confusion over the identity of *Aeolothynnus* of Ashmead (1903) versus the concept of *Aeolothynnus* used by Turner (1908). As discussed in detail by Kimsey (1999) Turner's concept of this genus actually was not congeneric with Ashmead's, and his designation of *A. cerceroides* as the type of *Aeolothynnus* included quite a different group of species. Unfortunately, some time earlier Ashmead (1899) had described the genus *Iswaroides,* based on the species *I. koebelei.* Turner never saw the type of *Iswaroides* and simply re-used Ashmead's description in the *Genera Insectorum* review of the subfamily Thynninae (Turner 1910c). Although these two type species are very different one from the other, there are a number of seemingly intermediate species, including one described below, and the distinctions between the two groups have never been clearly resolved.

The difficulty with these generic groupings has several origins. A large part of the confusion comes from the nomenclatural chaos created by Turner, Ashmead, and Rohwer. This confusion is in turn compounded by our incomplete knowledge of the species diversity. A six-week collecting trip to Western Australia yielded twenty species of *Iswaroides/Thynnoturneria,* yet only five species have been described from this part of Australia. Based on examination of museum collections there are very few widespread species in this group. "*Thynnoturneria*" *cerceroides* appears to occur in Western Australia, South Australia, and Northern Territory. However, this entity is actually a cluster of at least three species, all closely resembling one another in coloration, gross morphology, and a peculiarly indented forefemur. However, each of these appears to have a discrete allopatric distribution, with one in SA, one in NT and one in WA.

Thorough phylogenetic analysis of all available species in these groups has revealed that there is no robust support for two genera as represented by *Iswaroides* Ashmead and *Thynnoturneria* Rohwer.

Materials and Methods

Specimens were studied *in situ* or were borrowed from the following: The Natural History Museum, London, S. Lewis; Hope Museum, Oxford University, C. O'Toole; Australian National Insect Collection, CSIRO, Canberra, ACT, I. Naumann and J. Cardale (CANBERRA); Bohart Museum of Entomology, University of California, Davis, S. L. Heydon (DAVIS), Naturhistorische Museum, Vienna, Austria, M. Fisher (VIENNA), and Western Australian Museum, Perth, Terry Houston (PERTH). Type repositories for the new species described below are indicated by the city name in capital letters in parentheses.

Males of twenty-five putative species were analyzed for this study, including the new species *I. robustus* described below, and representatives of three other genera, *Acanthothynnus sannae* Turner, *Aspidothynnus fossulatus* Turner, and *Epactiothynnus opaceiventris* Turner. An asterisk (*) indicates primary types examined for this study. Fifteen of the species given in the data matrix are morphospecies assigned by a letter name, because there does not appear to be an available species name.

Nearly all of the types of species placed in these genera are in The Natural History Museum, London. It has not been possible to restudy these types in light of the re-evaluation of *Iswaroides* and *Thynnoturneria*. Ordinarily this paper would not have been published without correct names or new species names being assigned to these taxa. However, there is considerable need to stabilized the generic framework in this speciose subfamily of wasps because of their roles both in the biodiversity of the Australian continent and their probable importance in population control of soil-dwelling scarab beetles, including imported dung beetles.

Phylogenetic analyses were conducted using the Hennig86 software (Ferris 1988), using branch swapping (mhennig and bb commands), followed by successive weighting and generation of a Nelson consensus tree (Fig. 1).

Phylogenetic Analysis

Character States

1. Labrum small, apical plate foreshortened, with row of subapical setae and narrow basal attachment (Fig. 4)(0); labrum large highly sclerotized and asetose except apical fringe, broadly attached, apex broadly rounded (Figs. 2, 3)(1).
2. Clypeal apex as broad or broader than medial eye width, apical margin broadly truncate (Figs. 2, 3)(0); apex narrow, often medially rounded, narrower than eye width (Fig. 4)(1).
3. Stipal fringe of setae long and dense, continuous along most of inner margin (Figs. 5, 6)(0); stipal fringe reduced to less than half of inner margin (1).
4. Stipes unmodified, stipal fringe occupying more than half of stipes (Fig. 5)(0); stipes shortened and posteriorly twisted, posterior half strongly cupped (Fig. 6)(1).
5. Prementum broad and parallel-sided (Figs. 6, 9)(0); prementum elongate (Fig. 5), often narrowed anteriorly (1).
6. Face flat or slightly concave between antennal socket and eye margin (0); area between antennal socket and eye longitudinally sunken and often polished and impunctate (1).
7. Occipital fossa and oral fossa narrowly separated by a ridge (Figs. 5, 7, 9)(0); broadly separated by flat or concave polished area (Fig. 6)(1).
8. Occipital carina meeting oral carina at an acute angle (Fig. 6)(0); reaching oral carina at an obtuse or right angle (Figs. 5, 7, 9)(1).
9. Vertex with red spot between hindocelli and upper eye margin (Fig. 8)(0); without red spot (1).
10. Pronotum strongly narrowed medially, depressed subapically (0); pronotum elongate medially and flat without transverse subapical depression (1).

Table 1. Character matrix for genera and species related to *Iswaroides*.

Taxon / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Epactiothynnus[1]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthothynnus[2]	1	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	1
Aspidothynnus[3]	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Iswaroides baccata	1	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	1	0
I. cerceroides	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0
I. illustris	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	1	0	0
I. koebelei	0	1	0	1	0	0	1	0	1	1	0	1	0	1	1	1	0	0
I. robustus	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	0
I. sanguinulentus	1	0	0	0	0	1	0	1	0	1	1	1	0	1	1	0	1	0
I. xerophila	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	1	0	0
I. species A	0	1	1	1	0	0	1	0	1	0	1	1	1	1	1	1	0	0
I. species B	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	1	0	0
I. species C	1	0	0	0	1	1	0	1	0	1	0	1	1	1	1	1	0	1
I. species D	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0
I. species E	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0
I. species F	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0
I. species G	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0
I. species H	1	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	0	1
I. species I	1	0	0	0	1	1	0	1	0	1	0	1	0	1	1	0	1	0
I. species J	0	1	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0
I. species K	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	1	0	0
I. species L	1	0	0	0	1	1	0	1	0	1	0	1	1	1	1	1	0	1
I. species M	1	0	0	0	1	1	0	1	0	1	0	1	0	0	1	1	0	1
I. species N	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0
I. species P	0	1	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0

[1] *Epactiothynnus opaceiventris* Turner.
[2] *Acanthothynnus sannae* Turner.
[3] *Aspidothynnus fossulatus* Turner.

11. Mesopleuron anteriorly rounded (0); anterior declivity margined by a vertical omaulus (1).
12. Mesopleuron with transverse scrobal groove extending anteriorly from scrobe (0); mesopleuron evenly convex without trace of scrobal groove (1).
13. Gastral tergum V evenly rounded subapically (Fig. 16)(0); subapical margin produced into an acute shelf-like ridge (Fig. 15)(1).
14. Gastral sternum V evenly rounded laterally (0); with lateral tooth (1).
15. Gastral sternum VI evenly rounded laterally (0); with lateral tooth (Figs. 15, 16)(1).
16. Volsella convex (0); concave at least on apical half and U-shaped in cross-section with digitus obscured (Fig. 22)(1).
17. Gonocoxal dorsal apex deeply emarginate medially appearing strongly bilobate (Figs. 18–20) or narrowly unilobate (Fig. 24)(0); apex convex medially, appearing trilobate (Fig. 17)(1).
18. Gonocoxal dorsal apex deeply emarginate medially appearing strongly bilobate or narrowly unilobate (0); apex broadly truncate (Fig. 23)(1).

Results

Representatives of the closely related genera *Acanthothynnus* Turner, *Aspidothynnus* Turner, and *Epactiothynnus* Turner were used in the analysis as outgroups to polarize the character states. These taxa all belong to the *Iswaroides* group of genera characterized in the males by having a partial or complete transverse carina or ridge at or near the apical margin of the epipygium. Males also have well-developed pe-

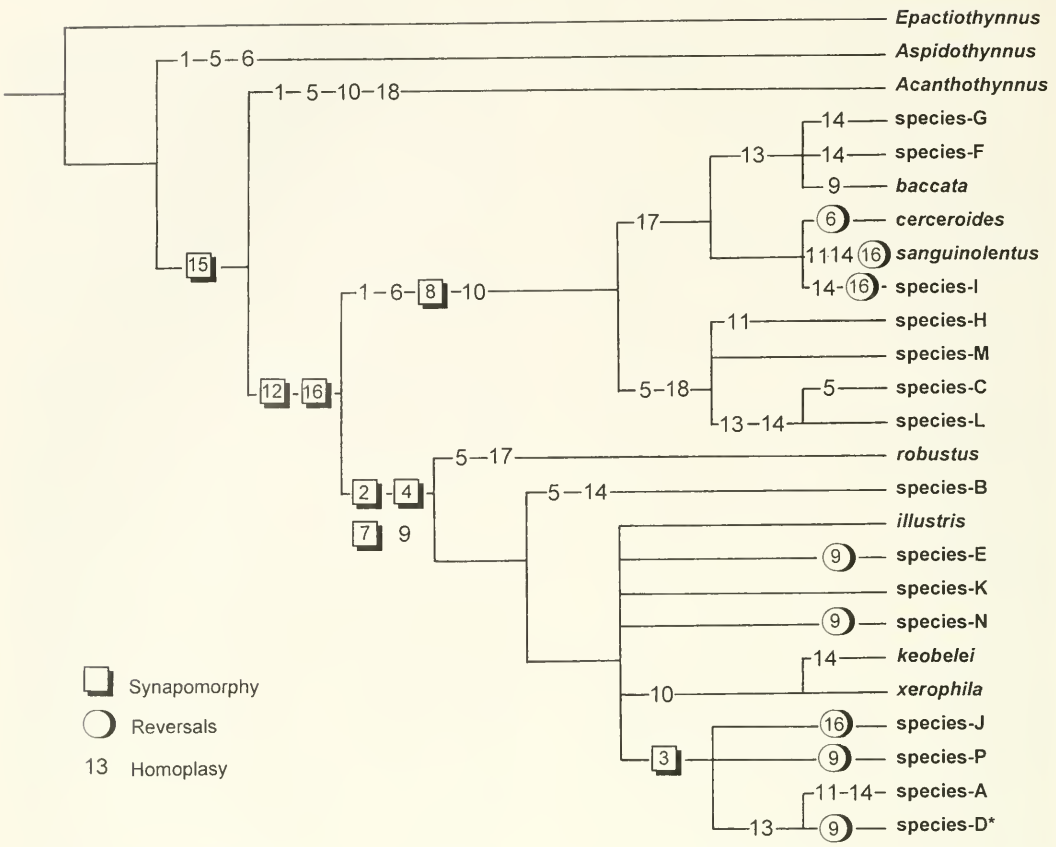


Fig. 1. Cladogram showing phylogenetic relationships among species of *Iswaroides*, *Epactiothynnus*, *Aspidothynnus*, and *Acanthothynnus*.

nis valves and a tridentate hypopygium. Females are characterized by the apical gastral tergum having a smooth, broadly or narrowly ovoid medial plate enclosed at least laterally by a carina and subtended medially by a long dense tuft of setae.

The character matrix, given in Table 1, was analyzed using intensive branch swapping and successive weighting, which yielded ten trees. A Nelson Consensus Tree generated from this last set of trees yielded the tree given in Fig. 1. The ci of the consensus tree was 74, with a retention index of 94. Most of the trees generated came from instability within the apical clades. The intent of this study was not to resolve species level relationships but rather to examine the stability of basal clades and to see if currently accepted generic groupings could be confirmed or repudiated.

The results of this study are twofold. First, there is little support for retaining *Thynnoturneria* and *Iswaroides* as separate entities. Although the types of each genus sort out consistently into two clades the basal rooting of these clades is weak, and they are not sufficiently well supported to justify their division into two genera. These two groups are referred to below as the *koebelei* and *cerceroides* clades. Second, the genus *Epactiothynnus* exhibited the ancestral condition in all of the characters examined for this study. This genus must be reexamined to determine if it is characterized by any apomorphies. If not, then the stability of all of the genera characterized

by the traits discussed above is in question. Given the results of this analysis, the genus *Thynnoturneria* Rohwer is synonymized under *Iswaroides* Ashmead as the junior name. The entire group, as *Iswaroides,* is rediagnosed below.

The *cerceroides* clade contains the type species of *Thynnoturneria* (*T. cerceroides*) as well as, *T. baccata, T. sanguinolentus* and species C, F, G, H, I, L, and M. The apomorphy supporting this clade is the occipital carina reaching the oral carina at an acute angle. Other characters that distinguish most members of this clade include the large shield-like labrum, polished and sunken area between the eye and the antennal socket and the dorsally flat and medially elongate pronotum. These latter features are also shared with *Aspidothynnus* and *Acanthothynnus* species.

The second clade is distinguished by one apomorphy—the strongly narrowed clypeal apex, as well as the loss of a red spot on the vertex in most, but not all species. Clade 2 contains *I. koebelei* (the type species of *Iswaroides*) *I. robustus, T. illustris, T. xerophila* and species A, B, D, E, J, K, N and P.

Collectively the *cerceroides* + *koebelei* clade is strongly supported by several apomorphies, including the lack of a scrobal groove, the mesopleuron evenly convex from dorsum to venter, and the peculiar volsella, which is relatively simple, U-shaped in cross section and lacks a visible digitus. The lateral tooth on gastral sternum VI distinguishes this basal clade, plus *Acanthothynnus,* from the other genera under consideration.

Successive weighting emphasized the value of characters 2–4, 7, 8, 12, 15, and 16, assigning these characters the highest values. In addition the following characters of apparent phylogenetic value turned out to be highly homoplaseous:

Character 1. In Thynnini the labrum is generally small and is rarely exserted below the clypeus. In the group of genera studied herein, as well as *Doratithynnus* Turner and *Encopothynnus* Turner, a large shield-like exserted labrum appears in a number of clades, including *Aspidothynnus* and the *T. cerceroides* clade. This feature also occurs in *Thynnus* Fabricius and several other unrelated genera.

Character 5. A narrow and elongate prementum occurs in both clades in basal branches, and is correlated with elongation of the entire tongue, which reaches its most extreme development in *robustus.*

Character 9. The presence of a red spot on the vertex is an enigmatic characteristic of about half the members of the *Iswaroides* group of genera, including *Acanthothynnus, Aeolothynnus* Ashmead, and *Psammothynnus* Ashmead. Two-thirds of the *I. koebelei* group appear to have lost these spots. However, for the purposes of this analysis reversing the coding on this feature improved the ci. The presence of spots in this clade is indicated as a reversal on the tree (Fig. 1).

Character 11. The degree of abruptness of the anterior mesopleural declivity varies considerably in this group. A vertical carina or ridge in this group frequently marks this declivity. However, this characteristic is highly variable among species and appears in both clades.

Character 14. Another highly variable characteristic of this group is the presence of a tooth on the sides of gastral sternum V. This tooth is generally associated with a transverse ridge. A similar ridge also occurs on subapical terga. The type species of *Iswaroides* (*I. koebelei*) and *Thynnoturneria* (*T. cerceroides*) represent the opposite extremes of this feature. In *I. koebelei* this carina is well-developed and protrudes shelf-like on segments III–VI (Fig. 15). Whereas in *T. cerceroides* there is no trace of a carina, although its position is indicated by a slight sulcus and swelling (Fig. 16). The development of this carina and sternal dentition occurs in a number of species in both clades, including *T. sanguinulentus* and *T. baccata* in the *T. cerceroides* clade and *T.*

xerophila in the *I. koebelei* clade. The degree of development also varies considerably from one species to the next, with many intermediates in development between the condition seen in *T. cerceroides* and that in *I. koebelei.*

Iswaroides Ashmead
(Figs. 2–19, 21–23)

Iswaroides Ashmead 1899: 50. Type species: *Iswaroides koebelei* Ashmead 1899: 50. Original designation.

Aeolothynnus Turner 1910c. Turner's mistaken concept of *Aeolothynnus* Ashmead.

Turnerella Rohwer 1910a: 349. Type species: *Thynnus cerceroides* Smith 1859: 34. Replacement name for *Aeolothynnus* Turner 1910c (nec Ashmead 1903). Preoccupied by Cockerell 1910c.

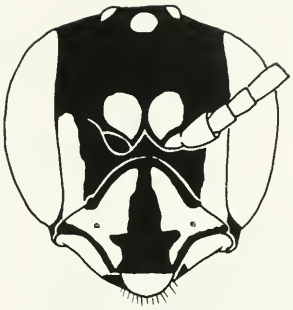
Thynnoturneria Rohwer 1910b: Replacement name for *Turnerella* Rohwer 1910a. Synonymized by Given 1960.

Eurohweria Turner 1911: 608. Invalid replacement name for *Aeolothynnus* Ashmead 1903. Synonymized by Rohwer 1911.

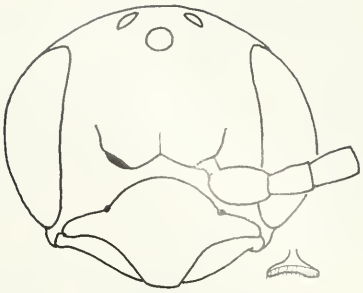
Male.—Body length 7–17 mm. *Head* (Figs. 2–7, 9): Face often longitudinally depressed between antennal sockets and clypeus; clypeus convex in profile apex broadly or narrowly truncate apically, wider or narrower than eye width in front view; labrum large, exserted and shield-like (Figs. 2,3) (as in *cerceroides*) or small and foreshortened, barely visible beyond clypeal apex (as in *koebelei,* Fig. 4); vertex unmodified; antennal lobes usually well developed, may be obsolescent in *cerceroides*; flagellomeres II–XI generally more than twice as long as broad, V–X each with two large tyloids; tongue generally short and unmodified, except in *robustus* (Fig. 10), stipes with elongate fringe of setae (Figs. 5, 6, 9); prementum generally parallel-sided; occipital and oral carinae meeting (Figs. 5, 7, 9), or widely separated (Fig. 6); vertex with small red spot between hindocelli and upper eye margin in some species (Fig. 8). *Thorax:* Pronotum often broad and flat dorsally, with strongly developed transverse frontal carina; mesopleuron strongly convex, without trace of transverse scrobal groove, often strongly declivitous anteriorly, with carinate edge in some species; forecoxa usually unmodified, but may be flattened and expanded laterally or posteriorly; forefemur usually unmodified, but may become large and shield-like as in *illustris*; metanotum obscured dorsally by scutellum and propodeum; hindcoxa with large basal carina on dorsal surface; forewing tcu-2 vein arising at base of SM-3 cell. *Abdomen:* Segments basally constricted (Figs. 15, 16); sternum I flat to strongly convex or lobate ventrally, as in *illustris*; terga I–VI and sterna II–V with transverse sulcus and/or carina subapically, carina becoming blade-like on apical segments, as in *koebelei* and *xerophila,* carina on apical sterna may end in acute lateral tooth (Figs. 15, 16), transverse sternal sulci obsolescent in *robustus*; sternum VI with acute lateral tooth, generally, but not always, associated with transverse sulcus/carina in all species; sternum VII apically tridentate, with teeth acute and medial tooth longest (Figs. 11–13); tergum VII broadly rounded, with subapical transverse carina laterally and apicomedially depressed and projecting somewhat ventrally. *Genital capsule* (Figs. 14, 17–19, 23): Penis valves spoon-shaped; parameres broadly rounded apically; volsella large and folded apically, appearing U-shaped in cross-section (Fig. 22), digitus obsolescent or small hidden behind outer wall of cuspis; aedeagus with long basal column topped by slender apical loop or strap; gonocoxa dorsally projecting and apicomedially unilobate, bilobate, weakly trilobate or truncate. *Color:* Black, often with yellow, whitish and/or red markings: abdomen may be entirely or partly red; wing membrane untinted to infumate.

Female.—Body length 4–9 mm. *Head:* Subovoid or elongate and narrowed posteriorly as in *xerophila* and *robusta,* with corresponding longitudinal groove beneath

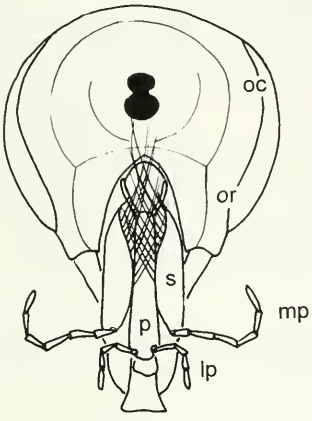
2. species-11



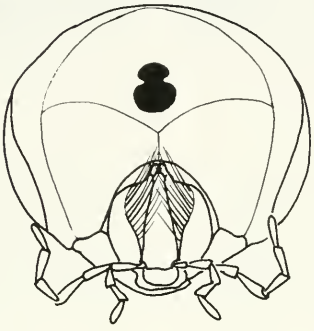
3. *cerceroides*



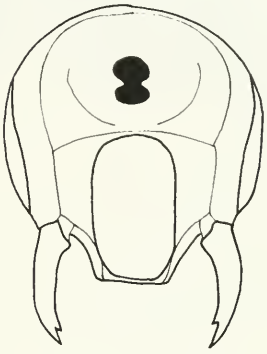
4. *keobelei*



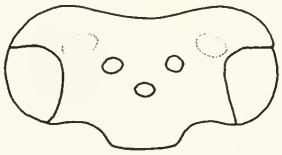
5. species-11



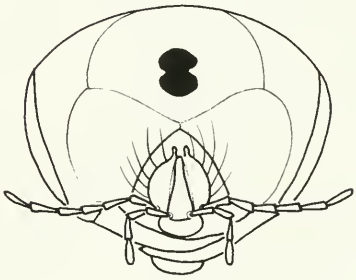
6. *keobelei*



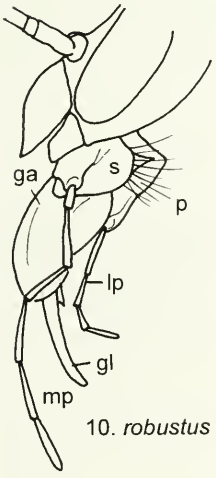
7. *cerceroides*



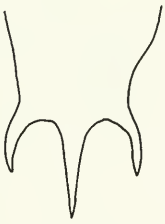
8. *sanguinolentus*



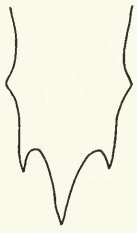
9. species-18



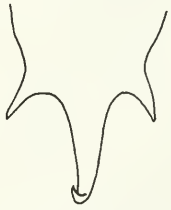
10. *robustus*



11. species-12



12. *cerceroides*



13. species-11

Figs. 2–13. 2–4, Front view of male face (4 with inset detail of labrum). 5–7, 9, Posterior view of male head, (tongue removed on 7). 8, Dorsal view of male head. 10, Lateral view of male head. 11–13, Ventral view of hypopygial apex. Abbreviations: ga = galea; gl = glossa; lp = labial palpus; m = maxillary palpus; oc = occipital carina; or = oral carina; p = prementum; s = stipes.

head on either side or surrounding occipital foramen; mandible slender, sickle-shaped, with shallow subapical notch. *Thorax:* Pronotum broadly subquadrate; scutellum narrowly visible, obscured by pronotum and scutellum. *Abdomen:* Tergum I with W-shaped transverse sulcus; tergum II with one or more transverse carinae; tergum V with laterotergite delimited by oblique groove and/or swelling, area adjacent to laterotergite often with short cresentic carina; tergum VI narrowly ovoid medially, margined laterally with longitudinal carina subtended by elongate tuft of setae (Fig. 21).

Distribution.—This genus is found throughout Australia.

Discussion.—*Iswaroides* belongs to the group of genera characterized by having a complete or partial transverse carina across the subapical margin of the male apical abdominal tergum, and spoon-shaped penis valves. Females have the apical tergum with an elongate ovoid medial plate delimited laterally by an oblique carina, subtended by a subapical tuft of elongate setae. Among these genera *Iswaroides* species can be immediately recognized in the males by the evenly and strongly convex mesopleuron and lateral tooth on sternum VI. However, the distinction of females in this group is problematic. There are too few females reliably associated with males in collections to distinguish between species level and generic characteristics.

The origin of the name *Iswaroides* is obscure. It seems fairly clear that Ashmead came up with this name as a modification of *Iswara* Westwood, meaning "like *Iswara.*" *Iswara* is a tiphiid genus in the subfamily Myzininae. Westwood (1845) does not indicate the origin of *Iswara.* This word is not Greek or Latin, and may be the name of a place or person. In any case Westwood treats the generic name as masculine. Therefore, Ashmead's modification—*Iswaroides* must also be treated as masculine.

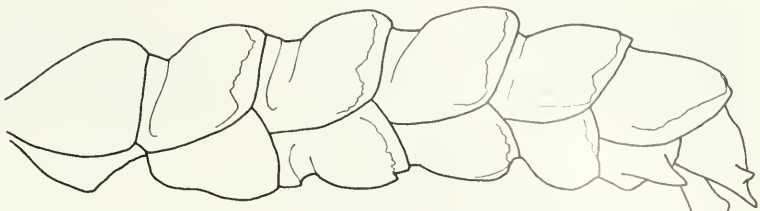
Included species.—Twenty-three species are placed in *Iswaroides: ablatus* (Turner) 1908* (*Thynnus*); *armiger* (Turner) 1908 (*Thynnus*); *baccatus* (Smith) 1868 (*Thynnus*); *centralis* (Turner) 1912 (*Thynnoturneria*); *cerceroides* (Smith) 1859 (*Thynnus*); *compressiceps* (Turner) 1911* (*Eurohweria*); *crenulatus* (Turner) 1910b (*Aeolothynnus*); *decipiens* (Westwood) 1845* (*Thynnus*); *eyrensis* (Turner) 1908 (*Thynnus*); *halophilus* (Turner) 1909 (*Thynnus*); *heinricheri* (Dalla Torre) 1897 (*Thynnus*) (replacement name for *Thynnus dimidiatus* Westwood 1845); *illustris* (Kirby) 1896 (*Rhagigaster*); *immitis* (Turner) 1911* (*Eurohweria*); *lachrymosus* (Turner) 1910a (*Aeolothynnus*); *myola* (Turner) 1911* (*Eurohweria*); *pentadontus* (Turner) 1911 (*Eurohweria*); *perturbatus* (Turner) 1910a (*Aeolothynnus*); *robustus* Kimsey **new species,** *sanguinolentus* (Turner) 1908* (*Thynnus*); *saundersi* (Turner) 1908 (*Thynnus*); *umbripennis* (Smith) 1859* (*Thynnus*) (= *Iswaroides koebelei* Ashmead 1899*); *xerophilus* (Turner) 1940 (*Aeolothynnus*).

Iswaroides robustus Kimsey, new species
(Figs. 10, 14, 21, 22)

Male.—Body length 17 mm; forewing length 13 mm. Head and thoracic punctation contiguous, appearing almost granular; tergal punctation laterally and ventrally shallow and 0.1–0.5 puncture diameters apart, dorsally smaller, shallow and 2–3 puncture diameters apart; malar space 1 MOD long; tongue greatly elongate, particularly the galeae and glossa (Fig. 10); flagellomere 1 1.9× as long as broad; flagellomere II length 3× breadth; flagellomere III 3.2× as long as broad; genital capsule (Figs. 14, 22). Body black, with yellow markings on clypeal margin, mandible, antennal lobe, pronotal anterior and posterior margins, tegula, parategula, medial spot on scutum and scutellum, metanotal posterior margin, and anteromedial spot on mesopleuron; small, lateral whitish spot on gastral terga II–IV; wings faintly brown-tinted; legs and antenna black.

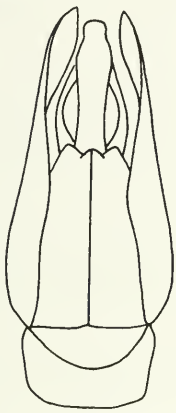
Female.—Clypeus with narrow apical truncation; vertex strongly arched, and narrowed; gena deeply and transversely in-

14. *robustus*

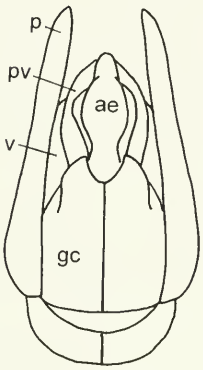


15. *koebelei*

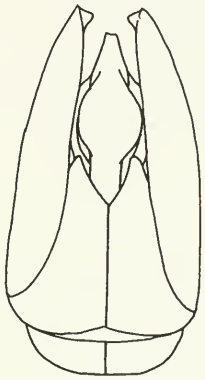
16. *cerceroides*



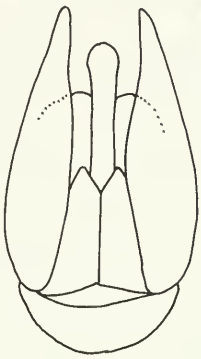
17. *sanguinolentus*



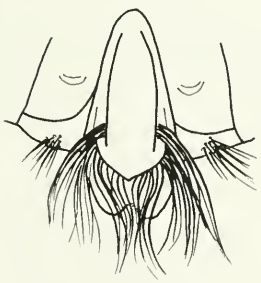
18. *koebelei*



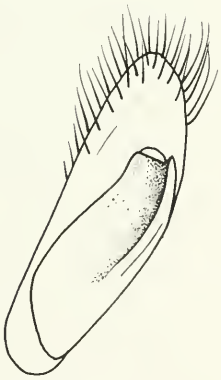
19. *illustris*



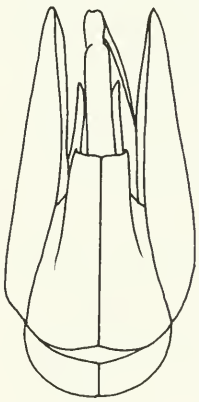
20. *Epactiothynnus*



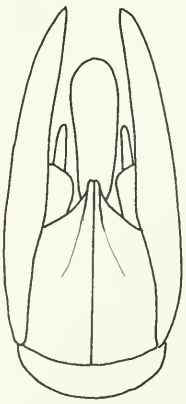
21. *robustus*



22. *robustus*



23. species-11



24. *Aspidothynnus*

Figs. 14–24. 14, Lateral view of genital capsule. 15, 16, Lateral view of male abdomen. 17–20, 23, 24, Male genital capsule (17, lateral view; 18–20, 23, 24, dorsal view). 21, Posterior view of apical segments of female abdomen. 22, Inner view of paramere and volsella. Species representatives of non-*Iswaroides* genera include: *Aspidothynnus fossulatus* Turner (Fig. 24) and *Epactiothynnus opaceiventris* Turner (Fig. 20). Abbreviations: a = aedeagus; gc = gonocoxa; p = paramere; pv = penis valves; v = volsella.

dented in U-shape below occiput, bulging, around oral fossa; occiput sunken; propleura bulging ventrally before forecoxa; propodeal posterior surface carina-edged laterally; mid and hindtibiae large and bulbous; foretarsus with long acute rake spines; midtibia with large short apically rounded spines on outer surface; forebasitarsus with apically rounded rake spines; hindtarsomeres with apical elongate, acute, rake spines; gastral tergum V deeply emarginate apicomedially, with small cresentic carina sublaterally; tergum VI elongate ending in angulate apex, with sublateral carinae delimiting smooth ovoid medial area, and subtended by elongate tuft of setae (Fig. 21); sternum VI horseshoe-shaped and deeply indented medially. Body color dark brown. Pubescence long, silky and pale.

Type material.—Holotype ♂: SOUTH AUSTRALIA, Kangaroo Is., Flinders Chase National Park, Rocky River, R. Wharton, (CANBERRA). Paratypes: 4 ♂ and 1 ♀: 1 ♂—"Australia" (VIENNA); 1 ♂—Eyre Hwy., 3 km e WA border, 12 Nov. 1987, T. F. Houston, ex *Eucalyptus* flowers (PERTH); 1 ♂—NSW: 100 km se Broken Hill, 32.51°S 141.37°E, 3–10 Oct. 1988, E. D. Edwards (CANBERRA); 1 ♂, 1 ♀—WA: 41 km e Madura, 31.55°S 127.25°E, 10 April 1981, D. J. Brothers (DAVIS).

Discussion.—This very distinctive species can be immediately recognized in both sexes by its unusually large size, and by the greatly enlarged male tongue. Females may be distinguished by having a short cresentic carina sublaterally on the subapical tergum; one transverse carina on tergum II; the head with the occiput sunken extending into a lateral genal groove; and the body covered with long pale silky setae. This species does not closely resemble any others in *Iswaroides*, in part because it lacks some of the specialized male characteristics seen in other species, including the well-developed transverse tergal and sternal carinae.

Acknowledgments

This study was made possible by the good graces of the collections and collection managers who made specimens available. My thanks also to Richard M. Bohart for helping to decipher the nomenclatural mess created by Turner, Ashmead, and Rohwer.

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BIOLOGY AND IMMATURE STAGES OF TWO SPECIES OF *HYDROPTILA* DALMAN (TRICHOPTERA: HYDROPTILIDAE) WHICH CONSUME *CLADOPHORA* (CHLOROPHYTA)

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Abstract.—Adults of *Hydroptila armata* Ross and *H. perdita* Morton (Trichoptera: Hydroptilidae) are often taken near streams, but information on their immature stages is lacking. Field-collected females laid eggs in the laboratory, and the larvae were reared to the adult stage. Larvae of both species consumed the liquid contents of individual cells of *Cladophora* (Chlorophyta) by piercing cell walls with their asymmetrical mandibles; early instars of *H. armata* also occasionally removed epiphytic diatoms and consumed them. Final instars of both species used algal filaments and silk secretions to construct cases, and *H. perdita* incorporated mineral and detrital material as well. Hypermetamorphosis was exhibited by each species; instars 1–4 were completed rapidly (2–6 d each), whereas the final stadium was of longer duration (9–16 d). Cases were attached to rocks and sealed prior to pupation. The total duration of the immature stages (egg, larva, pupa) under laboratory conditions (~20°C; 12:12 L/D) was 43–54 d for *H. armata* and 36–47 d for *H. perdita*. The immature stages are described.

Key Words: *Hydroptila armata, Hydroptila perdita,* microcaddisflies, aquatic insects, streams, algae, *Cladophora,* rearing

The immature stages of most species of Trichoptera are unknown despite ample attention by aquatic entomologists (Wiggins 1990, 1996). The species richness of microcaddisflies (Hydroptilidae) is second only to the Limnephilidae, with some 311 species reported from North America, Mexico, and Greenland (Morse 1993). A number of studies of larval biology and morphology of Nearctic species have been conducted (Ross 1944, Flint 1962, Flint and Herrman 1976, McAuliffe 1982, Vaillant 1984, Huryn 1985, Resh and Houp 1986, English and Hamilton 1986, Keiper et al. 1998, Keiper and Foote 1998), but descriptions of the immature stages which include the early instars have not been published. The Australian (Wells 1985), European (Nielsen 1948, Lepneva 1964, Solem 1972), and Japanese (Ito and Kawamura 1980) hydroptilid faunas are somewhat better understood.

Hydroptila Dalman contains over 100 species from North America (Morse 1993). Ross (1944) gave brief descriptions of the fifth instars of a number of species from Illinois, including *H. armata* Ross; the larva of *H. perdita* Morton was previously unknown. Adults of both species have been collected near streams (Ross 1944, Huryn and Foote 1983). Herein, we give biological and morphological information on *H. armata* and *H. perdita* obtained during laboratory rearings initiated from eggs laid by field-collected females.

Materials and Methods

To initiate rearing, adult females were taken with an aspirator from a sheet illuminated with an ultraviolet collecting light. Collecting vials (containing live females) were placed in a cooler with ice for transport back to the laboratory. *Hydroptila armata* was taken at the Hocking River, 1 km west of Nelsonville, Ohio (Athens Co.), and *H. perdita* was collected at the Little Miami River near Fort Ancient State Memorial (Ohio, Warren Co.).

In the laboratory, adults were narcotized with CO_2, and females were pierced through the mesosternum with a number 3 insect pin when signs of revival were noted. This caused some females to dump their eggs in a mass or chain, and we transferred these adults with their eggs to individual Petri dishes containing stream water. Females were allowed to float on the surface overnight until the completion of egg laying, and then preserved in 70% ethanol. Eggs were also allowed to float on the surface until larval eye spots appeared. Small masses of the filamentous alga *Cladophora* (Chlorophyta) collected from local streams were rinsed gently with distilled water to remove any invertebrates present, placed in the dishes, and the eggs submerged among the filaments. All Petri dishes were kept at ~20° C, and a 12:12 light : dark photoperiod maintained.

Larval behavior and feeding habits were observed at 6–50× with a Wild M5 dissecting microscope. Early instars (1–4) were determined by direct observation of molts. If enough larvae were available, representatives of each stadium were collected, fixed with Kahle's solution, and preserved in 70% ethanol following the methods of Wiggins (1996). The water was changed every other day, and the algal food source was replenished when necessary. Upon attaining the fifth (and final) instar, larvae were transferred to aerated rearing chambers (Keiper and Foote 1996) with stream water, small rocks, algae, and mineral and detrital material to facilitate case building.

Illustrations of the immature stages were initiated by obtaining a tagged image format (TIF) computer file using a low light camera (Optronics Engineering DEI-470) mounted on the Wild scope or a Leica compound microscope, and Image Pro Plus image analysis software for IBM. To acquire images at high power (100×), larvae were placed on a microscope slide to which a drop of glycerol was added and viewed with the compound scope. TIF images were printed and traced or used as a reference. Measurements were obtained using the Image Pro Plus software. Physical descriptions and head capsule width measurements were taken from 10 specimens for each instar, and other measurements were obtained from one specimen per instar.

Results

Biology of *Hydroptila armata* Ross

Approximately 100 eggs were obtained from the single *H. armata* induced to oviposit. Eggs were ovoid, colorless, without surface markings, and measured 0.150 × 0.135 mm (n = 15). Eggs were laid in chains, but spread singly over the surface of the water when the female was placed in the Petri dish. After 5 d of incubation, the developing embryo was observed clearly through the chorion, and dark eye spots became apparent after 6 d. After 7 d, dark setae were seen pressed against the inside of the chorion, and the first hatching occurred approximately 12–24 h after these setae were first observed. The remaining eggs hatched after 8 d, giving an incubation period of 7–8 d at ~20°C.

First instars moved among filaments of *Cladophora*, and appeared to feed almost exclusively on the apical cells of filaments. Larvae consumed the contents of algal cells by piercing them with their mandibles and removing the fluid protoplast. Early instars executed up to 25 bites before piercing a cell and obtaining its contents. One larva

grasped a cell with its mandibles in a symmetrical orientation, and quickly pulled its head away, tearing off a piece of the cell wall. This was discarded, and the larva resumed its series of bites.

Several larvae used their mandibles to occasionally remove epiphytic diatoms from filaments of *Cladophora* by placing the tips of their mandibles on both ends of the elliptical frustule, and prying it from the filament. Larval guts were consistently dark green from consumption of *Cladophora* protoplast, therefore it appears that diatoms constituted only a minor proportion of the diet of *H. armata.*

Fifth instars constructed cases composed of two valves, similar in shape to that illustrated by Wiggins (1996). Approximately 85% of the case material was short filaments of *Cladophora,* and only 15% was mineral particles bound together by silken secretions. Larvae occasionally "unstitched" the ventral edge of their cases, and added more material before reattaching the valves, thus accommodating the increasing girth of the abdomen as the larva accumulated food reserves (see Nielsen 1948).

Completed cases were approximately 3.4 mm in length, and ranged from 0.735–0.887 mm in height. Larvae laid down layers of silken secretions to form a cocoon on the inside walls of cases. These bouts of activity were executed an undetermined number of times prior to attaching and sealing their cases, each lasting approximately 3–10 minutes. Bouts were spread out over a period of several days.

Fifth instars pierced individual cells within filaments of *Cladophora* with their asymmetrical mandibles (see below); the right mandible is pointed and was used to puncture individual cells, while the left one has a serrated inner edge, and apparently was used to maintain a grip on the cell when a biting motion was executed. During a bite, each mandible adducted to different degrees. The point of the right mandible was inserted into the cell wall and adducted strongly. In contrast, the inner edge of the left mandible adducted slightly, pressing the cell to the mouth of the larva. A bite was facilitated with a counterclockwise twist of the head (when viewed dorsally) approximately 20–30°, which applied leverage to the force of the right mandible. Epiphytic diatom consumption by final instars was not observed.

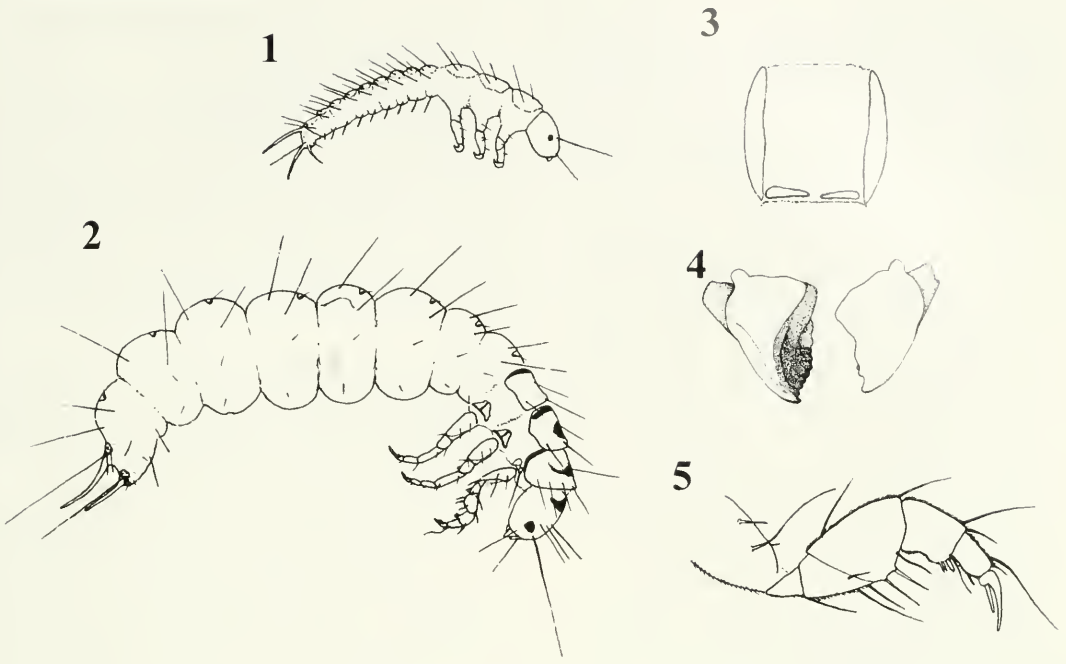
The duration of the five instars under laboratory conditions was 4–6, 5–6, 4–6, 4–6, and 12–16 d, while the pupal duration was 7–8 d. The total duration of the immature stages (egg, larva, and pupa) was 43–54 d, with a larval/pupal period of 36–48 d.

Biology of *Hydroptila perdita* Morton

Three females induced to oviposit produced 11, 115, and 175 ($\bar{x}$ = 100.3) eggs, respectively, which were scattered loosely over the water surface. The first eggs hatched after 9–12 d of incubation. The newly-hatched larvae immediately began to feed mostly on the contents of the apical cells within filaments of *Cladophora.* All instars fed in a manner similar to that described for *H. armata,* although epiphytic diatom consumption was never observed.

Case building commenced within 24 h of molting into the fifth instar. This species appeared to be generalized in its case material requirements, utilizing algal filaments, sand grains, and detrital material in approximately equal amounts. One individual even incorporated what seemed to be a blue carpet or clothing fiber which fell into the rearing chamber. Otherwise, construction and shape resembled that of *H. armata.* Larvae attached their cases to stones within the rearing chambers or the rearing chamber wall and floor, and sealed them prior to pupation.

The duration of the five instars under laboratory conditions was 2–4, 3–4, 2–3, 2–3, and 9–12 d, while the pupal duration was 9–10 d. The total duration of the immature stages (egg, larva, and pupa) was 36–47 d, with a larval/pupal period of 27–36 d.



Figs. 1–5. *Hydroptila armata*. 1, Third instar, lateral view. 2, Fifth instar, lateral view. 3, Prosternum, anterior up. 4, Left and right mandibles, ventral view. 5, Fore leg, lateral view.

Description of Larval *Hydroptila armata* Ross

First two instars with colorless, unmarked head capsules, black eye spots, and black setation; bodies dorsoventrally flattened. Instars three and four with slight but noticeable darkening of sclerites. Body round in cross section. Head capsule and thoracic nota covered with dense pile visible at high magnification only. Head capsule dimensions given in Table 1.

First instar.—Total length, 0.692 mm; prothorax, 0.070 mm; mesothorax, 0.073 mm; metathorax 0.086 mm; abdominal segment 1, 0.034 mm; segment 2, 0.034 mm; segment 3, 0.033 mm; segment 4, 0.035 mm; segment 5, 0.030 mm; segment 6, 0.032 mm; segment 7, 0.038 mm; segment 8, 0.040 mm; segments 9 and 10, 0.042 mm.

Second instar.—Measurements not taken, but size increase proportional to first instar.

Third instar.—Total length, 2.260 mm; prothorax, 0.224 mm; mesothorax, 0.258

Table 1. Head width range, median, and factor of increase[1] of *H. armata* and *H. perdita*.

Instar	*H. armata*			*H. perdita*		
	Head Width (mm)		Factor of Increase	Head Width (mm)		Factor of Increase
	Range	Median		Range	Median	
I	0.090	0.090		0.090	0.090	
II	0.105–0.120	0.113	1.26	0.120	0.120	1.33
III	0.150	0.150	1.33	0.150	0.150	1.25
IV	0.180–0.195	0.188	1.25	0.180–0.195	0.188	1.25
V	0.210–0.225	0.218	1.16	0.210–0.240	0.225	1.20

[1] Obtained by dividing the head width median of the current instar by that of the previous instar.

mm; metathorax, 0.224 mm; abdominal segment 1, 0.125; segment 2, 0.125; segment 3, 0.143; segment 4, 0.110 mm; segment 5, 0.130 mm; segment 6, 0.121 mm; segment 7, 0.139 mm; segment 8, 0.130 mm; segments 9 and 10, 0.192 mm (Fig. 1).

Fourth instar.—(Only one specimen obtained, and placed in 70% ethanol which appears to have caused the specimen to contract.) Total length, 1.861 mm; prothorax, 0.258 mm; mesothorax, 0.177 mm; metathorax, 0.157 mm; abdominal segment 1, 0.078 mm; segment 2, 0.089 mm; segment 3, 0.063 mm; segment 4, 0.051 mm; segment 5, 0.087; segment 6, 0.066 mm; segment 7, 0.113 mm; segment 8, 0.128 mm; segments 9 and 10, 0.172 mm.

Fifth instar.—Total length, 4.022 mm; prothorax, 0.094 mm; mesothorax, 0.102 mm; metathorax, 0.137 mm; abdominal segment 1, 0.085 mm; segment 2, 0.102 mm; segment 3, 0.137 mm; segment 4, 0.599 mm; segment 5, 0.609 mm; segment 6, 0.665 mm; segment 7, 0.466 mm; segment 8, 0.381 mm; segments 9 and 10, 0.463 mm. Head capsule and thoracic nota with yellowish-brown base color and black banding pattern (Fig. 2); recently-molted fifth instars without dark banding pattern on thoracic sclerites and head capsule. Two small triangular prosternal sclerites posteriorly, concolorous with other sclerites (Fig. 3). Mandibles asymmetrical and without setae; right mandible pointed apically with small subapical tooth; left one with inner edge finely serrated (Fig. 4). Fore tarsus with a long subapical dorsal seta, approximately twice length of tarsal claw; basal seta of tarsal claw extending past midpoint of claw (Fig. 5). Meso- and metapleura with dark brown sutures. Abdomen of the mature larva approximately two to three times girth of thorax; sclerites of abdominal segments 9 and 10 pale; anal claw dark brown. Dorsal chloride epithelia elliptical and faint. Primary setae very dark basally, gradually becoming light brown apically.

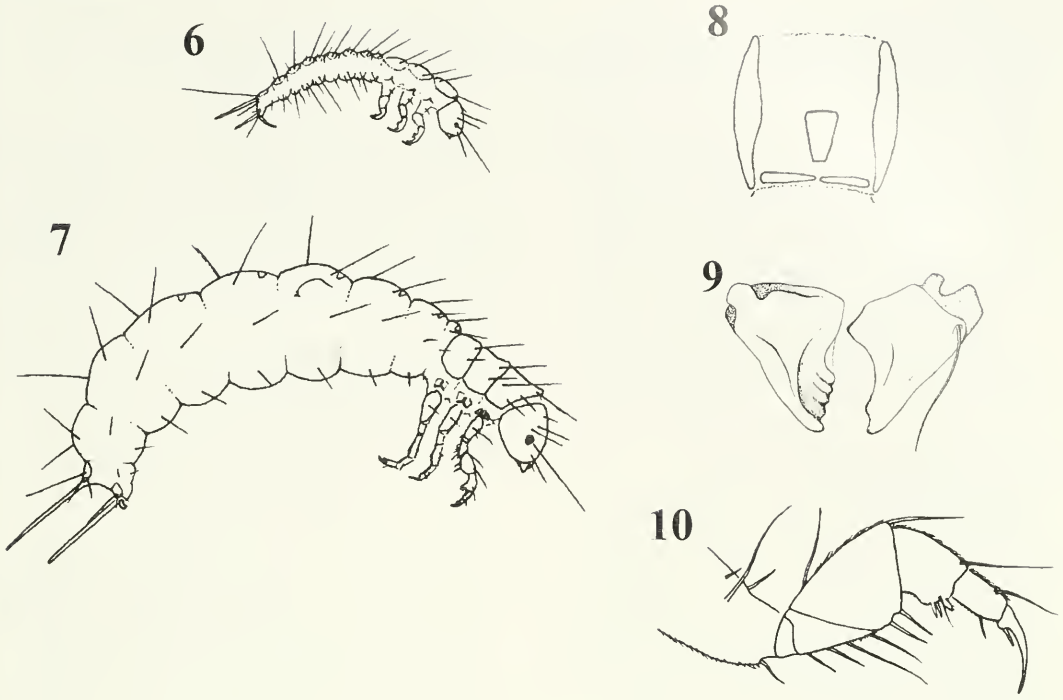
Description of Larval *Hydroptila perdita* Morton

Bodies of instars one and two somewhat flattened dorsoventrally. Instars three and four with slight but noticeable darkening of sclerites; body round in cross section. Head capsule and thoracic nota covered with dense pile visible at high magnification only. Head capsule dimensions given in Table 1.

First instar.—Total length, 0.570 mm; prothorax, 0.070 mm; mesothorax, 0.070 mm; metathorax, 0.050 mm; abdominal segment 1, 0.021 mm; segment 2, 0.024 mm; segment 3, 0.033 mm; segment 4, 0.039 mm; segment 5, 0.027 mm; segment 6, 0.023 mm; segment 7, 0.025 mm; segment 8, 0.036 mm; segments 9 and 10, 0.036 mm; central gill, 0.135 mm; lateral gills, 0.150 mm (Fig. 6). Head capsule uniformly dull yellow, unmarked, and darker than rest of body; eye spots dark; setae black.

Second, third, and fourth instars.—Measurements not taken, but size increase proportional in successive instars. Head capsule yellowish, darkening slightly with age.

Fifth instar.—Total length, 2.62 mm; prothorax, 0.150 mm; mesothorax, 0.125 mm; metathorax, 0.140 mm; abdominal segment 1, 0.070 mm; segment 2, 0.170 mm; segment 3, 0.215 mm; segment 4, 0.305 mm; segment 5, 0.285 mm; segment 6, 0.265 mm; segment 7, 0.215 mm; segment 8, 0.250 mm; segments 9 and 10, 0.165 mm; central gill, 0.458 mm; lateral gills, 0.410 mm. Head capsule uniformly dull yellow and unmarked (Fig. 7). Three prosternal sclerites (Fig. 8); posterior sclerites triangular and narrow; central sclerite quadrangular and tapering posteriorly; concolorous with other sclerites. Mandibles asymmetrical; right pointed apically, with small subapical tooth, and one seta at posterolateral corner; left with coarsely serrated inner edge, and without setae (Fig. 9). Fore tarsus with short subapical dorsal seta, approximately length of tarsal claw; basal seta of



Figs. 6–10. *Hydroptila perdita*. 6, First instar, lateral view. 7, Fifth instar, lateral view. 8, Prosternum, anterior up. 9, Left and right mandibles, ventral view. 10, Fore leg, lateral view.

tarsal claw extending up to midpoint of claw (Fig. 10). Meso- and metapleura with dark brown sutures. Abdomen of mature larva approximately twice the girth of thorax. Sclerites of abdominal segments 9 and 10 and anal claw brown. Dorsal chloride epithelia elliptical and faint. Primary setae very dark basally, gradually becoming light brown apically.

Pupa.—Appears similar to those species described by Nielsen (1948) and Ito and Kawamura (1980). Total length, 2.32 mm; head width, 0.63 mm; antennal length, 1.28 mm.

Discussion

Only a few descriptions of larval *Hydroptila* are available. Ross (1944) separated groups of species from Illinois based on color of head and thoracic sclerites, but cautioned that color patterns are variable within species. His key is presently unreliable due to species whose larvae are unknown, new distributional records, and recent reports of species new to science from eastern North America (e.g., Houp et al. 1998). *Hydroptila armata* is easily distinguished from *H. perdita* based on the dark color pattern of the head and thorax, lack of a central prosternal sclerite, presence of a long subapical tarsal seta, and lack of setae on the posterolateral corner of the right mandible of *H. armata*. No characters were found to separate the early instars of these species, however the early instars of *H. itoi* Kobayashi have brown thoracic and abdominal sclerites with long setae (Ito and Kawamura 1980) which contrast those observed on *H. armata* and *H. perdita*.

Few morphological characters appear to be of general use for separating final instar *Hydroptila*. Prosternal sclerites appear variable in number (2 or 3) between species; if present, the shape of the central sclerite varies from trapezoidal (*H. perdita*), diamond-shaped (*H. tineoides* Dalman) (Niel-

sen 1948 as *H. femoralis* Eaton), and pentagonal (*H. coweetensis* Huryn) (Huryn 1985). Mandible morphology of *Hydroptila* may be the most useful character for species identification of larvae because shape and setation appear to differ among species (Nielsen 1948, Lepneva 1964, Ito and Kawamura 1980, Huryn 1985, Keiper 1998, Keiper and Foote 1998, this study). Further larva-adult associations through rearings coupled with detailed distributional records should facilitate the compilation of regional keys to species based primarily on mandible morphology for *Hydroptila* and possibly other microcaddisfly genera.

Previous investigations indicated that some degree of trophic specialization occurs in hydroptilid larvae (Nielsen 1948, Resh and Houp 1986). Recently, Keiper et al. (1998) demonstrated that *H. waubesiana* Betten and *Oxyethira pallida* (Banks) completed the larval/pupal period when given only monocultures of certain algal taxa, whereas larvae consuming other algal monocultures did not. Although we gave larvae only *Cladophora* during this investigation, we suspect that *H. armata* and *H. perdita* exhibit a similar degree of feeding specialization. The mandibles of each species appear similar to those of *H. waubesiana* (Keiper 1998), and are apparently specialized for piercing individual cells of green algae.

The collection localities for adults utilized during this study corroborate statements by Ross (1944) that each of these species prefers moderate-sized streams. Ross (1944) collected *H. armata* fifth instars in Illinois streams, but the larval microhabitat of *H. perdita* remains unknown. Our observations of larval behavior and feeding habits suggest that larvae of *H. perdita* inhabit rock substrates with ample growths of *Cladophora,* as this is where similar species have been taken (e.g., Huryn 1985, Wells 1985, Keiper 1998, Keiper and Foote 1998). Further collections of fifth instar *Hydroptila* for laboratory rearings in areas where *H. perdita* adults are encountered are needed to confirm this.

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TWO NEW GENERA AND SPECIES OF MEALYBUGS (HEMIPTERA: COCCOIDEA: PSEUDOCOCCIDAE) THAT PRODUCE PLANT GALLS

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Abstract.—In the mealybug family Pseudococcidae, only 23 species in 14 genera are known to be gall formers. The purpose of this paper is to describe two new South American genera and species that cause galls; namely ***Miconicoccus ruebsaameni*** and ***Quadrigallicoccus lauracearum.*** These mealybugs are legless and apparently are related to *Antonina* Signoret. They are the first gall-forming mealybugs known from the continental land mass of the New World. A review of gall-forming mealybugs from other parts of the world is also presented.

Key Words: gall-forming mealybugs, galls, Coccoidea, Pseudococcidae, new genera, new species, *Miconicoccus ruebsaameni, Quadrigallicoccus lauracearum,* South America, review

Gall producing scale insects have long been a subject of general interest (Beardsley 1984), particularly in Australia where a significant proportion of the Coccoidea biota produces galls (Gullan 1984). Scale insects in 10 families are gall formers, including the Margarodidae (2 species in 2 genera), Pseudococcidae (23 species in 14 genera), Eriococcidae (more than 100 species in at least 21 genera), Kermesidae (4 species in 3 genera), Coccidae (1 species in 1 genus), Asterolecaniidae, Cerococcidae, and Lecanodiaspididae (most species in these families form at least a pit or depression on their host, some form galls that enclose the body of the female), Beesoniidae (all species of this family form galls some of which are colonial), and Diaspididae (16 species in 12 genera).

There is a surprising paucity of true gall formers within the Pseudococcidae; in fact, outside of Hawaii only 5 other species of mealybugs are known to form definite galls, i.e., *Cataenococcus gallicolus* (Mamet), *Eurycoccus sternlichti* Williams, *Grewiacoccus gregalis* Brain, *Lantanacoccus sauroides* Williams and Granara de Willink, and *Pseudoripersia turgipes* (Maskell). In Hawaii, 11 species in 5 genera are known to produce galls (Beardsley 1984) (actually Beardsley did not mention *Pseudococcus antricolens* Ferris and *Gallulococcus tenoriori* Beardsley but included 2 species in his figures that do not produce galls).

Since information on gall-forming mealybugs has not been reviewed since Beardsley (1984), we felt that it would be useful to provide a summary as part of the introduction. While writing this section and examining illustrations of each species, we were struck by the fact that many of the true gall-forming species have one or more mor-

phological modifications that are shared by other unrelated gall-forming mealybugs and apparently relate to the gall-forming habit. These apparent, gall-mediated, morphological characteristics include: a series of large conical setae on at least the posterior apex of the abdomen, often these are modified anal-lobe cerarii; a pear-shaped body with the posterior apex narrowest; hind legs that are enlarged or modified in some manner; the posterior apex of the body that is sclerotized and may be modified. Species that fall in this category are as follows: *Gallulococcus tenorioi* has the body pear shaped; it forms shallow pocket galls on the leaves of its *Metrosideros* (Myrtaceae) host (Beardsley 1971). *Grewiacoccus gregalis* has enlarged hind coxae and the posterior apex of the abdomen is covered with enlarged conical setae; it forms a blunt leaf gall on the undersides of its *Grewia* (Tiliaceae) host in South Africa (Brain 1918). *Lantanacoccus sauroides* has numerous dorsal enlarged setae; it forms deep, hardened gall-like depressions on the leaves of *Lantana* (Verbenaceae) in Haiti and Jamaica (Williams and Granara de Willink 1992). *Nesopedronia acanthocauda* (Beardsley) has the anal-lobe cerarii so enlarged that they form a continuous row of setae across the apex of the abdomen and has only the hind two pair of cerarii present; the gall is formed from a rolled fern pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Nesopedronia crypta* (Beardsley) has the anal-lobe cerarii so enlarged that they form a continuous row of setae across the apex of the abdomen; the gall is formed from a rolled fern pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Nesopedronia dura* (Beardsley) has the posterior apex of the abdomen sclerotized and developed into a small pygidial-like flap; it forms a hard, gall-like roll at the apex of each affected pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Pseudoripersia turgipes* has dorsal conical setae, large robust legs, and a large anal-lobe cerarius with many setae; it produces galls on *Casuarina* (Casuarinaceae) by causing branchlets to become distorted and curl around the body of the insect; it occurs in Australia (Williams 1985). *Phyllococcus oahuensis* (Ehrhorn) has a heavily sclerotized and flattened posterior portion of the abdomen that is specialized for sealing the entrance to the gall; it forms erect galls on the leaves of *Urera* (Urticaceae) (Ferris 1948).

We were surprised to find that several true gall-forming species seem to have no unusual morphological modifications. Within this category of mealybug gall former we found species that have gall-forming congeners with morphological modifications. Species without obvious modifications include: *Cataenococcus gallicolus* which forms galls on the twigs of an unidentified creeper in Madagascar (Mamet 1954). *Eurycoccus sternlichti* Williams forms galls on the twigs of *Quercus ithuburensis* (Fagaceae) that are up to 8 cm long and 3 mm thick in Israel (Williams 1958). *Nesopedronia cibotii* (Beardsley) does not always cause host deformation; when galling occurs it is limited to the edges of the pinnules which are curled on its *Cibotium* (Dicksoniaceae) host (Beardsley 1957). *Nesopedronia hawaiiensis* (Ferris) forms a rosette-like gall of fern pinnules (Beardsley 1959) on its *Dicranopteris* (Gleicheniaceae) host. *Pseudococcus antricolens* produces finger-like galls on the upper surface of the leaves of *Santalum freycinetianum* (Santalaceae) in Hawaii (Ferris 1948). *Pseudococcus gallicola* Ehrhorn produces pocket galls on the upper surface of *Santalum* (Santalaceae) leaves (Ferris 1948). *Pseudotrionymus multiductus* Beardsley forms a gall by rolling the entire leaf near the midrib of its *Syzygium* (Myrtaceae) host (Beardsley 1959). *Pseudotrionymus refertus* (Ferris) forms a gall by rolling the leaf margins of its *Eugenia* (Myrtaceae) host (Beardsley 1959).

Ohiacoccus cryptus Beardsley was reported as forming galls (Beardsley 1984) but as far as we can determine it does not cause any host deformation. According to

the original description of Beardsley (1971) "All the specimens were found at the bases of leaf petioles where these were tightly appressed to the twigs and where the insects [were] imbeded in thick tomentum which is characteristic of the *typica* variety of ohia."

There are several species of mealybugs that cause host deformation but are not obligate gall formers and are not specialized morphologically for gall habitation. They include: *Hypogeococcus festerianus* (Lizer y Trelles) on *Cereus* (Cactaceae) and *Echinopsis* (Cactaceae) in Argentina (Williams and Granara de Willink 1992); *H. pungens* Granara de Willink mainly on *Cereus* and *Eriocerius* (Cactaceae) in Argentina and Brazil (Williams and Granara de Willink 1992); *Maconellicoccus hirsutus* (Green) on many hosts in many parts of the world (Williams 1996); *Nipaecoccus viridis* (Newstead) on several hosts in Jordan (Sharaf and Meyerdirk 1987); *Phenacoccus herreni* Cox and Williams on *Manihot esculenta* (Euphorbiaceae) in South America (Cox and Williams 1981); *Phenacoccus manihoti* Matile-Ferrero on *Manihot esculenta* and several other hosts in South America (Cox and Williams 1981); *Phenacoccus parvus* Morrison on many hosts throughout the world (Williams, personal observations).

In this paper we describe two genera and two species from Central and South America that are the first gall-producing mealybugs to be described from continental land masses in the New World. These genera can be distinguished from others in the area by the following key modified from couplets 2 and 3 of the key to genera in Williams and Granara de Willink (1992):

2. Minute ducts present ventrally in distinct oval to round areas posterior of hind spiracles . . . . . *Chaetococcus* Maskell
– Minute ducts absent ventrally posterior of hind spiracles; sometimes with minute pores in this area 3a
3a. Antennae each with 2 or 3 segments 3b
– Antennae each represented by unsegmented sclerotized area 3c
3b. Anal ring either on surface at posterior end of abdomen or at base of anal tube, always with setae at least as long as diameter of ring . . . . . *Antonina* Signoret
– Anal ring on surface, situated about twice its diameter from posterior end of body, with setae shorter than diameter of ring . . . . . *Paludicoccus* Ferris
3c. Posterior end of body pointed. Anal ring at end of anal tube, with 6 setae. Multiple circuli present. Cluster of minute pores absent from each side of vulva. . . . . *Miconicoccus* Williams and Miller, n. gen.
– Posterior end of body rounded. Anal ring on body surface, not at end of anal tube, without setae. Circuli absent. Cluster of minute pores present on each side of vulva. . . . . *Quadrigallicoccus* Williams and Miller, n. gen.

Methods

Terminology in the descriptions follows that of Williams and Watson (1988) and Gimpel and Miller (1996). Sclerotized slits are present laterad of the hind legs of the first instar and laterad of the middle legs of the second-instar male of *Quadrigallicoccus lauracearum*. We have not observed these structures before and are uncertain of their function. Measurements and numbers are from 10 specimens when available, and are given as an average followed by the range in parentheses. Depositories of specimens are: The Natural History Museum, London (BMNH); National Museum of Natural History, Beltsville, MD (USNM); R. M. Bohart Museum, Davis, CA (UCD); Muséum National d'Histoire Naturelle, Paris (MNHN). The coauthors are equally responsible for the research and production of this paper.

Results

Miconicoccus Williams and Miller, new genus

Type species.—*Miconicoccus ruebsaameni* Williams and Miller.

Diagnosis.—*Adult female:* Body rotund; posterior apex sclerotized; segmental line between segments VII and VIII heavily sclerotized, with associated apophysis. Cerarii represented by paired spine-like setae at apex of opening of anal tube. Trilocular

pores uncommon; multilocular pores present. Oral-collar tubular ducts of *Antonina* type with partial external tube surrounding internal vestibule; oral collars abundant. Multiple circuli present. Anal ring with numerous pores, invaginated in long tube that has second ring near opening of invagination; anal-ring setae apically capitate. Legs absent. Spiracles without pores in atrium. Antennae represented by unsegmented, sclerotized area containing several setae.

First instar: With 2 sizes of trilocular pores. Without ostioles. Anal-ring setae enlarged, with blunt apices. Enlarged setae on dorsum of segment VII. Cerarii present on posterior 2 abdominal segments. With 2 or 3 circuli. Apex of abdomen sclerotized.

Etymology.—The name of this genus is formed from the generic name of the plant host *Miconia* (Melastomataceae) and the Latin *coccum* meaning seed or scale insect. *Miconicoccus* is a masculine noun.

Notes.—This genus is remarkably similar to *Antonina* Signoret and undoubtedly is closely related, but differs by having multiple circuli on the ventral abdomen, antennae represented by an unsegmented sclerotized area, and paired, conspicuous spine-like setae on either side of the opening to the anal tube. *Antonina* lacks circuli or has only 1, has antennae that are 2- or 3-segmented, and lacks paired setae at apex of opening of anal tube. The first instars of these genera are virtually identical except that *Miconicoccus* has 2 or more circuli and lacks ostioles. *Antonina* rarely has circuli, but when present there is only 1, and always has at least the posterior pair of ostioles (Yang and Kosztarab 1967).

Miconicoccus ruebsaameni Williams and Miller, new species

Type material.—The holotype adult female is mounted singly on a slide with the following information: Left label "Peru, Tarapoto/ on Miconia ibaguensis/ galls/ E. H. Rübsaamen/ X. 1902 No 95/gall no 548/ see Marcellia 1907 6:164/ 165; right label "*Miconicoccus*/ *ruebsaameni*/ Williams & Miller/Holotype/C.I.E./B.M.196" (USNM). In addition there are 3 other adult female paratypes, 2 immature paratypes, and 4 first instar paratypes in USNM; there is 1 adult female paratype and 1 immature paratype in BMNH. All material is apparently from the same location although one USNM slide indicates "On Miconia/ Dr. Edw. Rubsaamen, coll./ rec'd 1907" while the second says "(larvae)/ on *Miconia* sp./ from *Edw. Rubsaamen*/ July 1, 08."

Notes.—This species was first mentioned by Rübsaamen (1907) for whom the species is named; he described the gall and compared the appearance of the anal wax with that of *Xylococcus filiferus* Löw. His description indicated that the gall is a knotty swelling on the branch and frequently is formed at a branch node.

Description.—*Adult female* (Fig. 1): Slide-mounted holotype 1.2 mm long, 1.0 mm wide; paratypes 1.3(0.8–1.6) mm long, 1.2(1.0–1.5) mm wide. Body nearly round, posterior apex sclerotized. Segments V and VI fused laterally.

Dorsum with trilocular pores present in small numbers in medial and mediolateral areas from head to segment V (on some paratypes triloculars were not located). Discoidal pores uncommon, in small numbers on submarginal areas of segments VI and VII, smaller than diameter of trilocular pore. Oral-collar tubular ducts of 3 variable sizes becoming smaller anteriorly, abundant over surface except absent from segment VIII. Setae on segment VIII abundant, posterior setae enlarged and spine-like; 1 or 2 setae on segment VII also enlarged; setae on remainder of dorsum very small and inconspicuous, becoming thinner anteriorly. Segments VII and VIII, and posterior part of VI sclerotized. Segmental line between segments VII and VIII heavily sclerotized with conspicuous internal apophysis; segmental line between segments VI and VII also heavily sclerotized, with smaller apophysis.

Anal ring represented by heavy band of more than 200 pores; present at end of in-

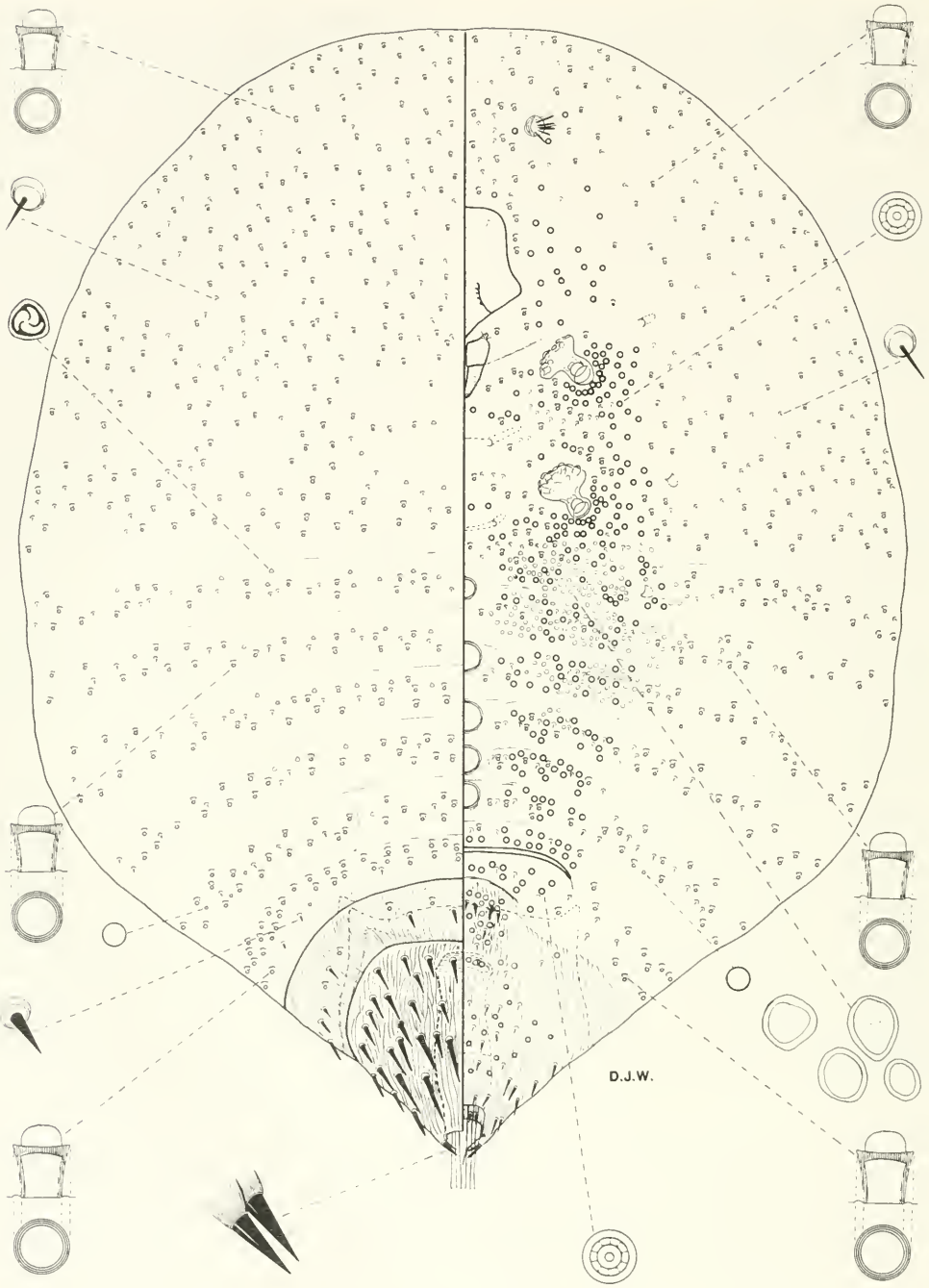

Fig. 1. *Miconicoccus ruebsaameni*. Adult female.

vaginated anal tube about 200 μ long; ring with 6 setae that protrude from end of tube, each seta with small distal club; anal tube with heavy band on venter anterior of exit to exterior.

Venter with multilocular pores of 2 sizes, smaller size on thorax and head and on segment VIII, larger size in medial and mediolateral areas from posterior thorax to segment VII, multilocular pores concentrated around spiracles, but not in atrium. Discoidal pores of 2 sizes, smaller size in small numbers in mediolateral areas of segments II to VI, with clear center, larger size in medial and mediolateral areas of metathorax to segment IV (some paratypes with pores absent on segment IV) with heavy rim and granular center. Trilocular pores absent. Oral-collar tubular ducts of same 3 sizes as on dorsum, abundant over surface except absent from segment VIII. Excluding anal-lobe seta, longest setae on segment VIII; anal-lobe seta anterior of anal opening, setae on rest of surface unusually small except on segment VIII where posterior and lateral setae are slightly enlarged. Segment VIII heavily sclerotized.

With 5 oval circuli, present on segments II to VI; middle circulus largest (1 paratype with middle circulus divided medially to form 2 lateral circuli). Labium 3-segmented, 84 μ long; paratypes 91(86–99) μ long. Antennae represented by unsegmented sclerotized knob containing 7 or 8 setae. Legs absent; usually with small dermal pockets in position of legs.

Notes: The above description is based on 5 specimens.

Immature female (probably third instar)(Fig. 2): Slide-mounted paratypes 0.9(0.7–1.1) mm long, 0.7(0.5–0.9) mm wide. Body nearly round, posterior apex sclerotized.

Dorsum with anal-lobe cerarii composed of 1 pair of conical setae. Trilocular and discoidal pores absent. Oral-collar tubular ducts of 3 variable sizes, becoming smaller anteriorly, abundant over surface except absent from segment VIII. Setae on segment VIII abundant, posterior setae enlarged and spine like; setae on remainder of dorsum very small and inconspicuous. Segments VII and VIII, and posterior part of VI sclerotized. Segmental line between segments VII and VIII heavily sclerotized with conspicuous lateral apophysis; segmental line between segments VI and VII also heavily sclerotized, without apophyses.

Anal ring represented by heavy band of more than 200 pores; present at end of invaginated anal tube 105(99–111) μ long; ring with 6 setae that protrude from end of tube; anal tube without heavy band anterior of exit to exterior.

Venter with multilocular pores of 2 sizes, smaller size near spiracles and on segment VIII, larger size in medial and mediolateral areas from just anterior of mouthparts posterior to segment VII; concentrated around spiracles, but not in atrium. Discoidal pores absent. Trilocular pores absent. Oral-collar tubular ducts of same sizes as on dorsum, abundant over surface except absent from segment VIII. Excluding anal-lobe seta, longest setae on segment VIII; anal-lobe seta near edge of anal tube opening; setae on rest of surface unusually small. Segment VIII heavily sclerotized.

With 4 or 5 oval circuli, present on segments II or III to VI; middle circulus largest. Labium about 56 μ long. Antennae represented by unsegmented sclerotized knob containing 7 or 8 setae. Legs absent; with small dermal pockets in position of legs.

Notes: The above description is based on 3 specimens.

First instar (gender not determined) (Fig. 3): Slide-mounted paratypes 0.5(0.4–0.5) mm long, 0.3(0.2–0.3) mm wide. Body elongate oval.

Dorsum with conspicuous cerarii on segments VII and VIII; those on segment VII each with 2 conical setae, 1 large trilocular pore, 1 small trilocular pore, and 1 discoidal pore; those on segment VIII each with 2 conical setae, 1 small-sized trilocular pore, and 1 discoidal pore; 2 thin setae and 1 or 2 associated trilocular pores on margin of

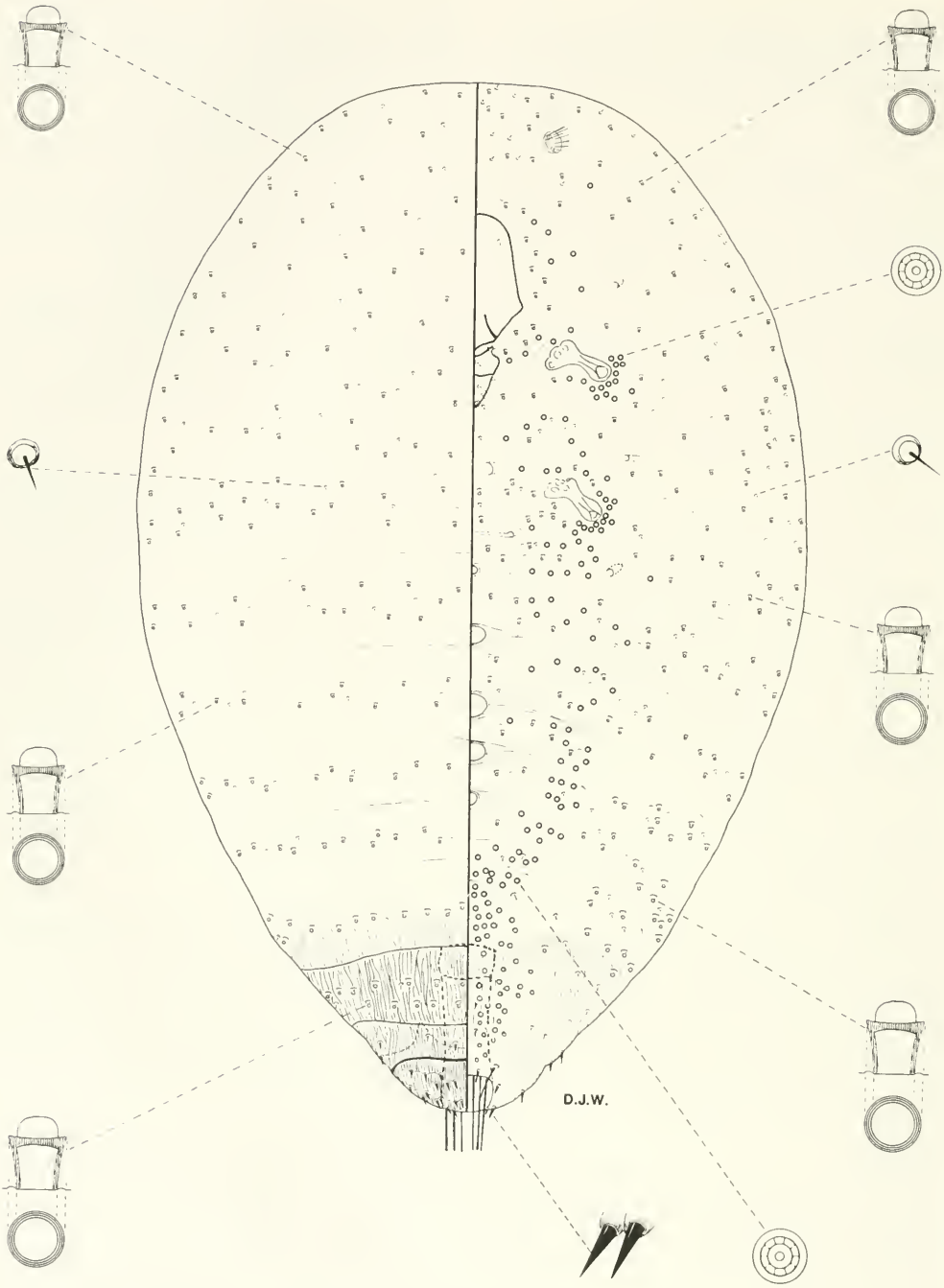

Fig. 2. *Miconicoccus ruebsaameni.* Third-instar female.

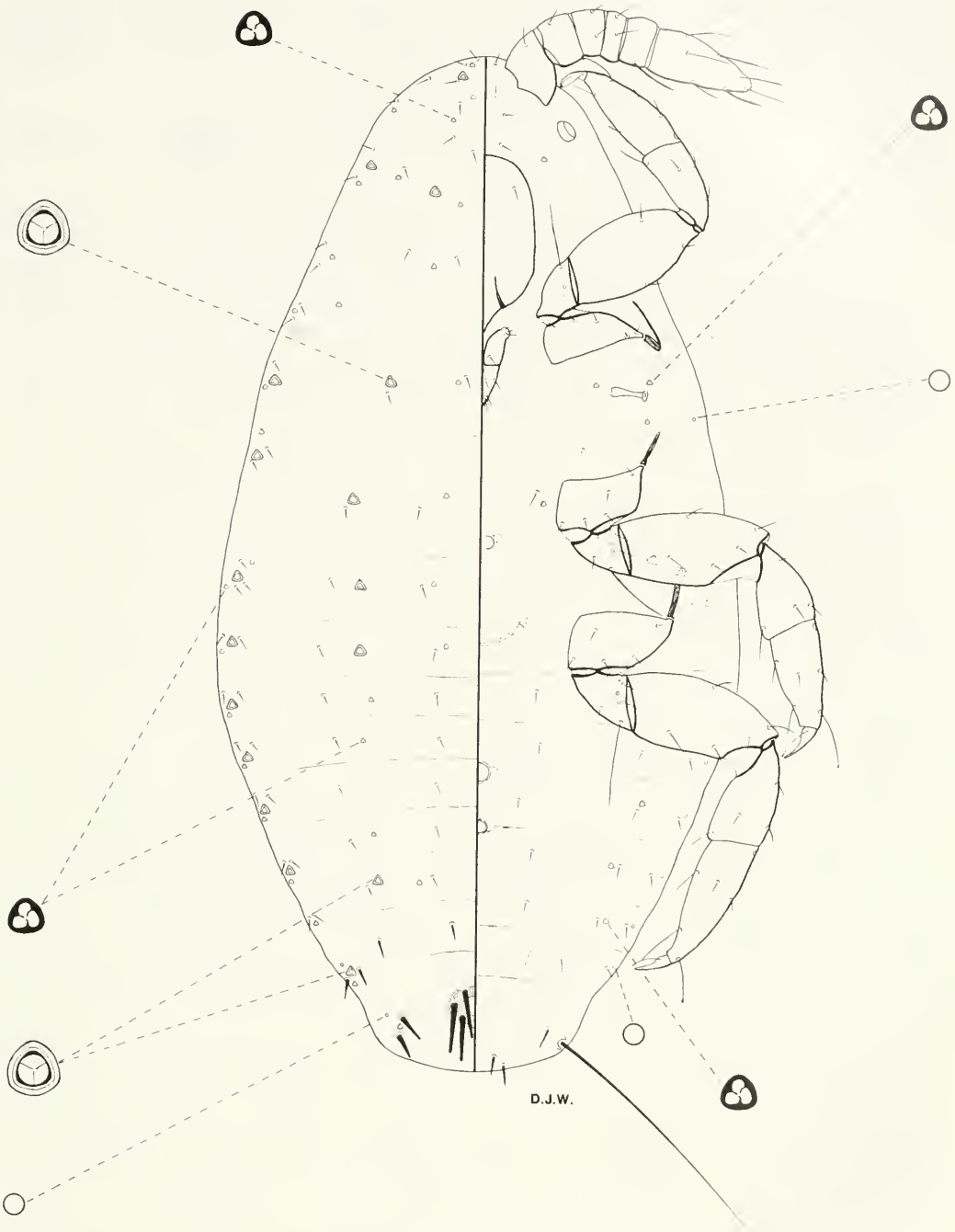

Fig. 3. *Miconicoccus ruebsaameni*. First instar.

most other abdominal segments forming inconspicuous cerarii. Trilocular pores of 2 sizes; larger size present in 2 pairs of interrupted longitudinal lines, 1 along body margin and associated with 2 setae on each segment except absent from segment VIII, 1 pair present in mediolateral lines, incomplete, present on head to abdominal segment I, and present on any or all of segments VI, VII, or VIII; smaller-sized triloculars arranged in 3 pairs of interrupted longitudinal lines, 1 along entire body margin, 1 present in mediolateral line on segments where larger size is absent, and 1 present in submedial line on head to abdominal segment I and 1 or 2 on abdomen. Discoidal pores absent except in posterior cerarii. Oral-collar tubular ducts absent. Setae absent from segment VIII except in cerarii; 1 pair of enlarged setae in medial area of segment VII; setae arranged in 3 pairs of longitudinal lines; marginal line composed of 2 setae which are homologous to cerarii in other mealybugs; mediolateral and submedial lines complete except absent from segment VIII; dispersed on head and thorax; with elongate anal-lobe seta. Segment VIII sometimes sclerotized.

Anal ring with 15(13–32) pores on each side of ring; with 6 enlarged, apically blunt setae. Anal tube absent.

Venter with trilocular pores present in mediolateral areas of any or all of segments IV, V, and VI; also present near spiracles. Discoidal pores present in lateral line with 1 on each side of each abdominal segment, also present laterad of each spiracle. Oral-collar tubular ducts absent. Longest setae on segment VIII; setae arranged in 3 pairs of longitudinal lines, submarginal, mediolateral, and submedial.

With 2 or 3 oval circuli, present on segments IV and V, sometimes present on segment III. Labium 62(57–67) μ long. Antennae 6-segmented, 128(124–136) μ long. Legs well developed, hind femur 49 μ long; hind tibia 35 μ long; hind tarsus 42 μ long; tibia/tarsus 0.8; femur/tibia 1.4; tarsal and claw digitules clubbed apically; claw without denticle.

Notes: The above description is based on 4 specimens.

Quadrigallicoccus Williams and Miller, new genus

Type species.—*Quadrigallicoccus lauracearum* Williams and Miller.

Diagnosis.—*Adult female:* Body rotund; vulva sometimes located at posterior apex of body on mounted specimens. Cerarii absent. Dorsum covered with trilocular pores similar to those of other pseudococcids; venter covered primarily with quadriloculars that have same structure as triloculars, but with 4 loculi; quinqueloculars most abundant near spiracles also similar to triloculars but with 5 loculi. Oral-collar tubular ducts present. Circulus absent. Anal ring either without pores or these very small and few; anal-ring setae absent. Legs absent. Spiracles without pores in atrium. Antennae represented by unsegmented, sclerotized area containing several setae.

Description.—*Adult male:* Body elongate. Penial sheath about ¼ length of body with sclerotization on both surfaces forming complete capsule. Ventral eyes set on protuberance; dorsal and ventral eyes each with depression around perimeter and small sclerotized dimples in lateral area of depression. Body with bristle-shaped setae only. Antennae primarily with elongated fleshy setae; capitate setae on 10th antennal segment absent or with very small club. Claw with digitules less than ¼ length of claw; with minute denticle near tip of claw. Abdominal tergites and sternites heavily sclerotized. With unusual minute tubular ducts.

Second-instar female: Ostioles restricted to anterior pair. Trilocular, quadrilocular, and quinquelocular pores with swirled pattern. Antenna 6-segmented. Oral collar tubular ducts present. Anal ring on dorsal surface removed from apex. Sclerotized slit present laterad of mid pair of legs.

Second-instar male: Trilocular, quadril-

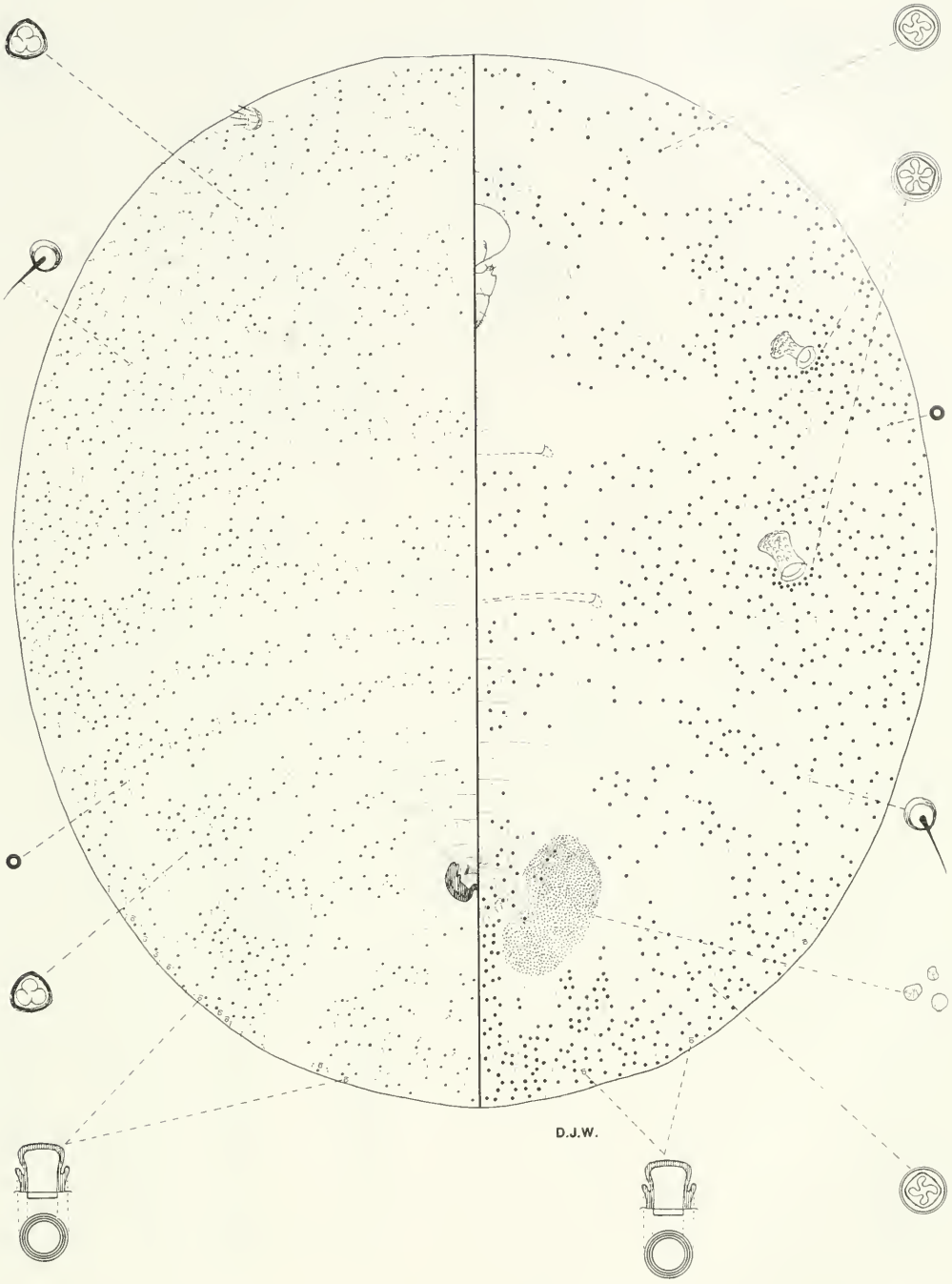

Fig. 4. *Quadrigallicoccus lauracearum.* Adult female.

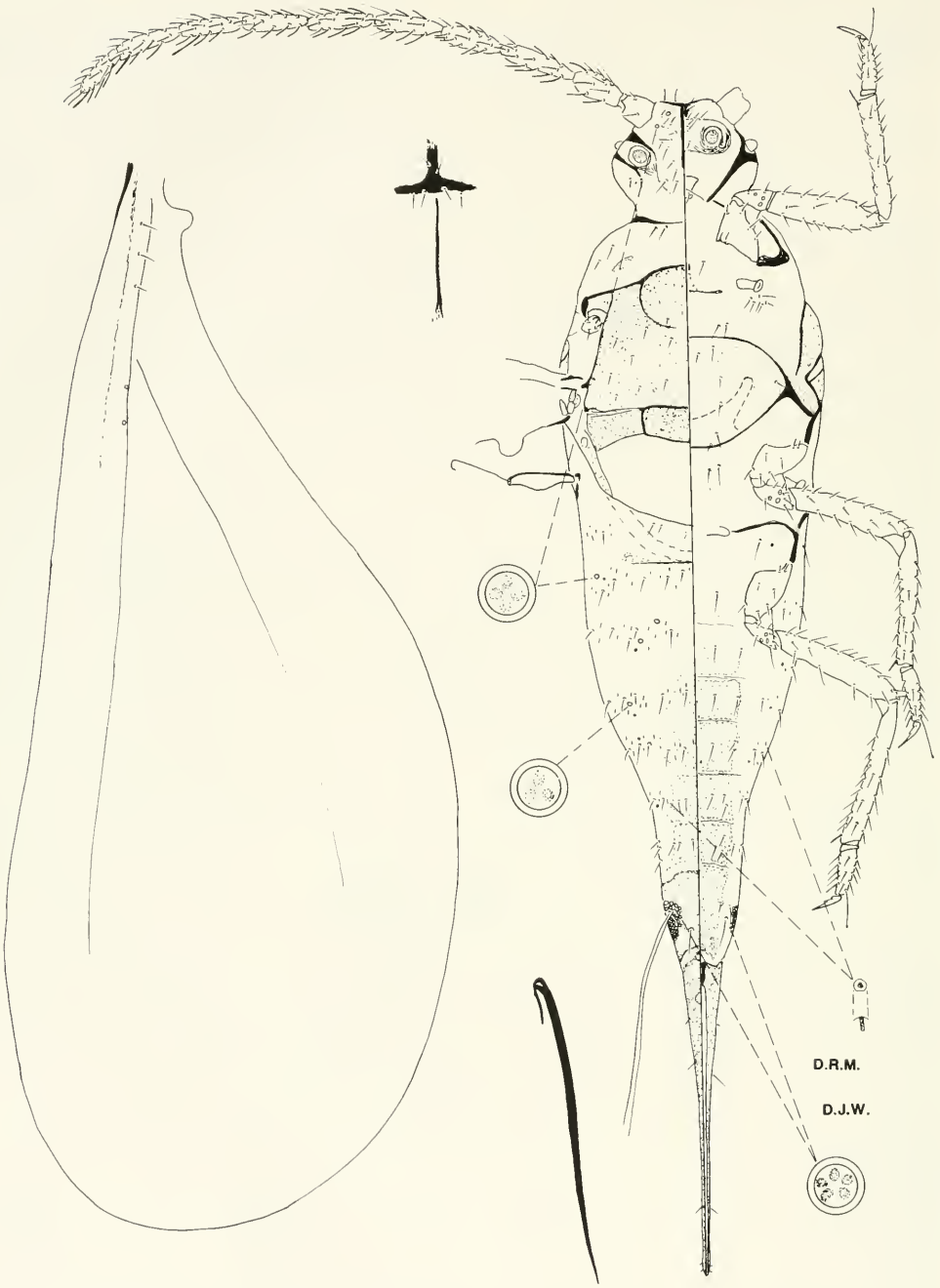

Fig. 5. *Quadrigallicoccus lauracearum.* Adult male.

ocular, and quinquelocular pores with swirled pattern. Antenna 7-segmented. Oral collar tubular ducts absent; minute tubular ducts present. Anal ring on dorsal surface near apex of abdomen. Sclerotized slit present laterad of hind pair of legs.

First instar: Without cerarii. With ostioles. Anal-ring setae absent; anal-ring pores

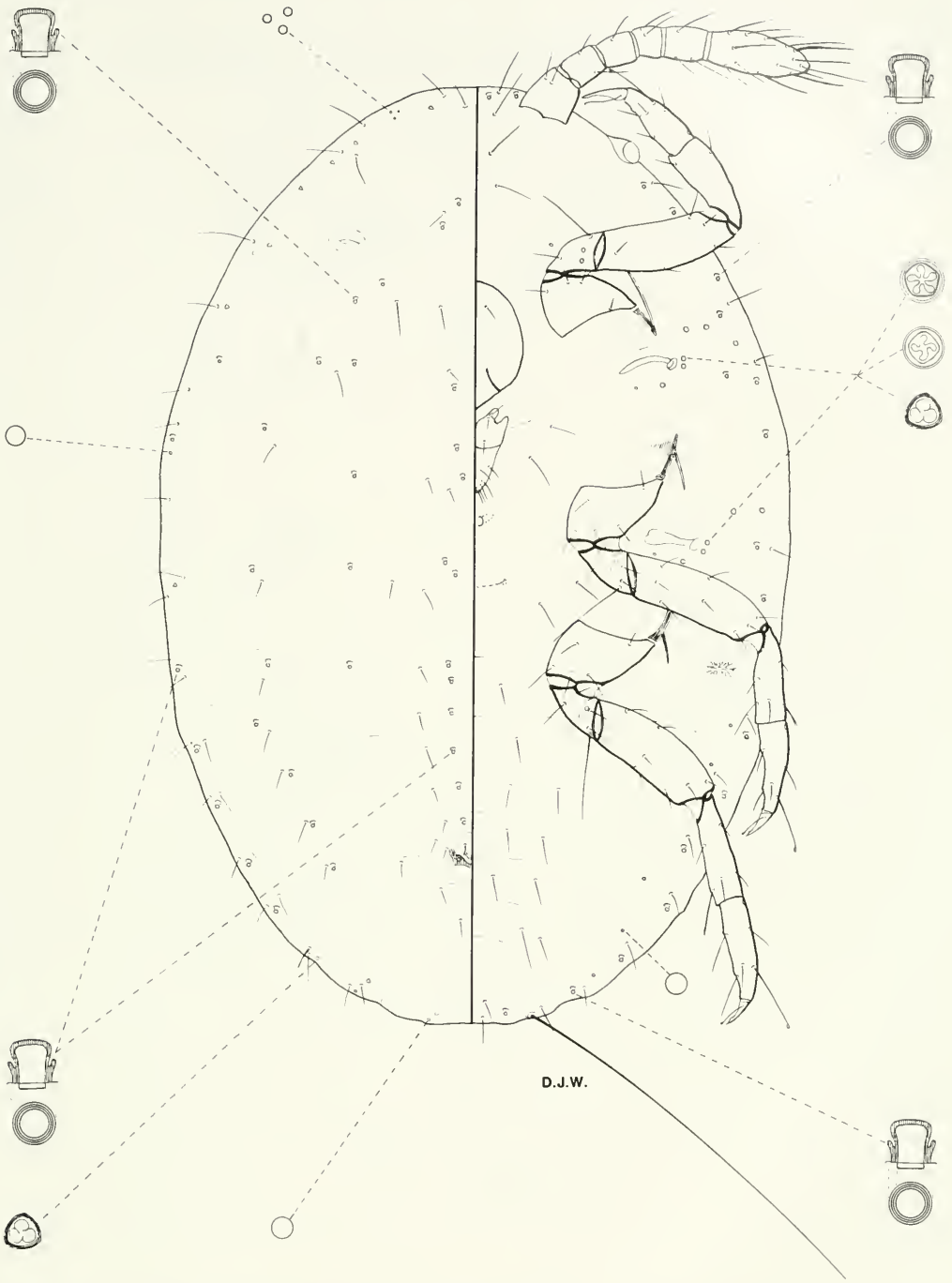

Fig. 6. *Quadrigallicoccus lauracearum.* Second-instar female.

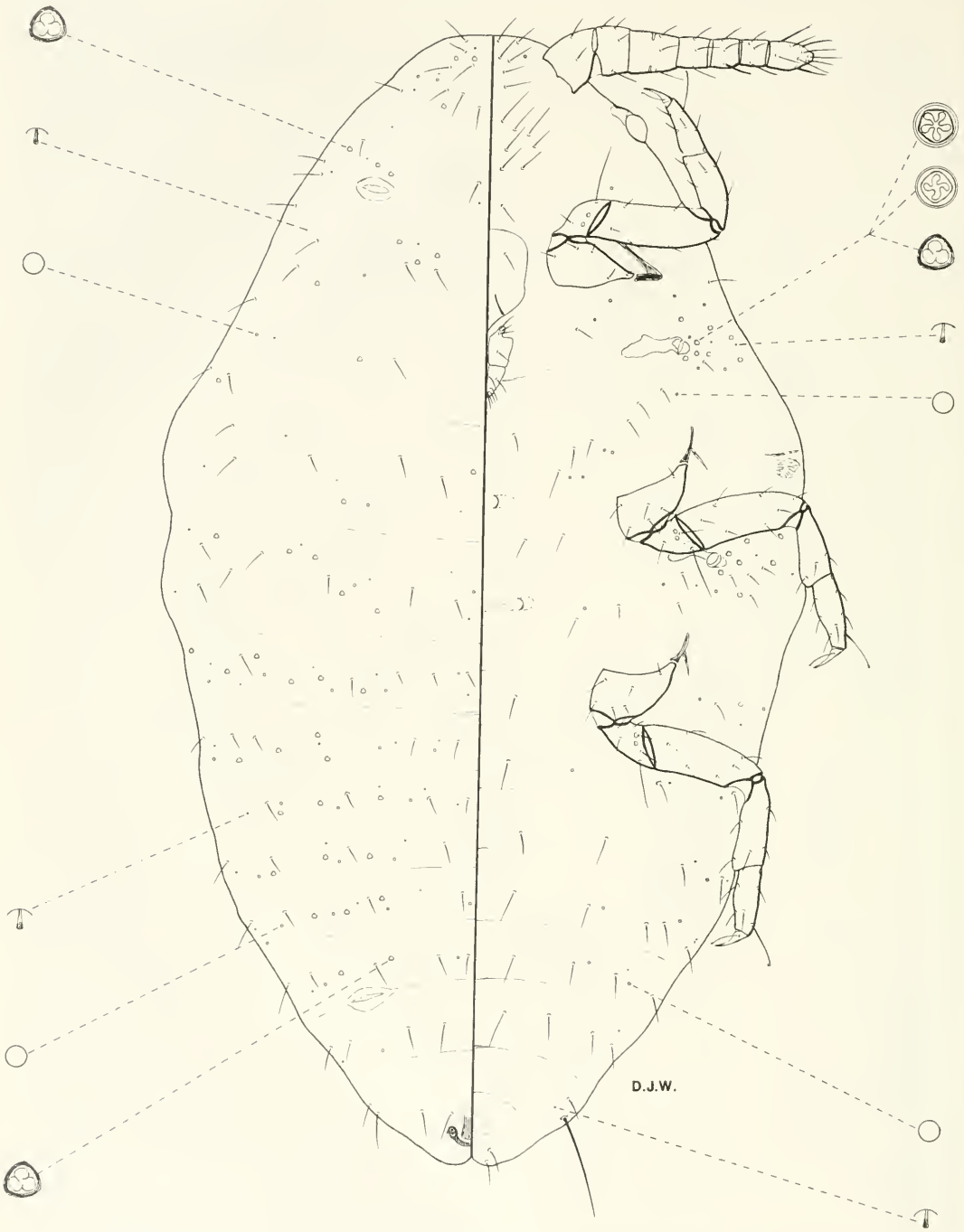

Fig. 7. *Quadrigallicoccus lauracearum.* Second-instar male.

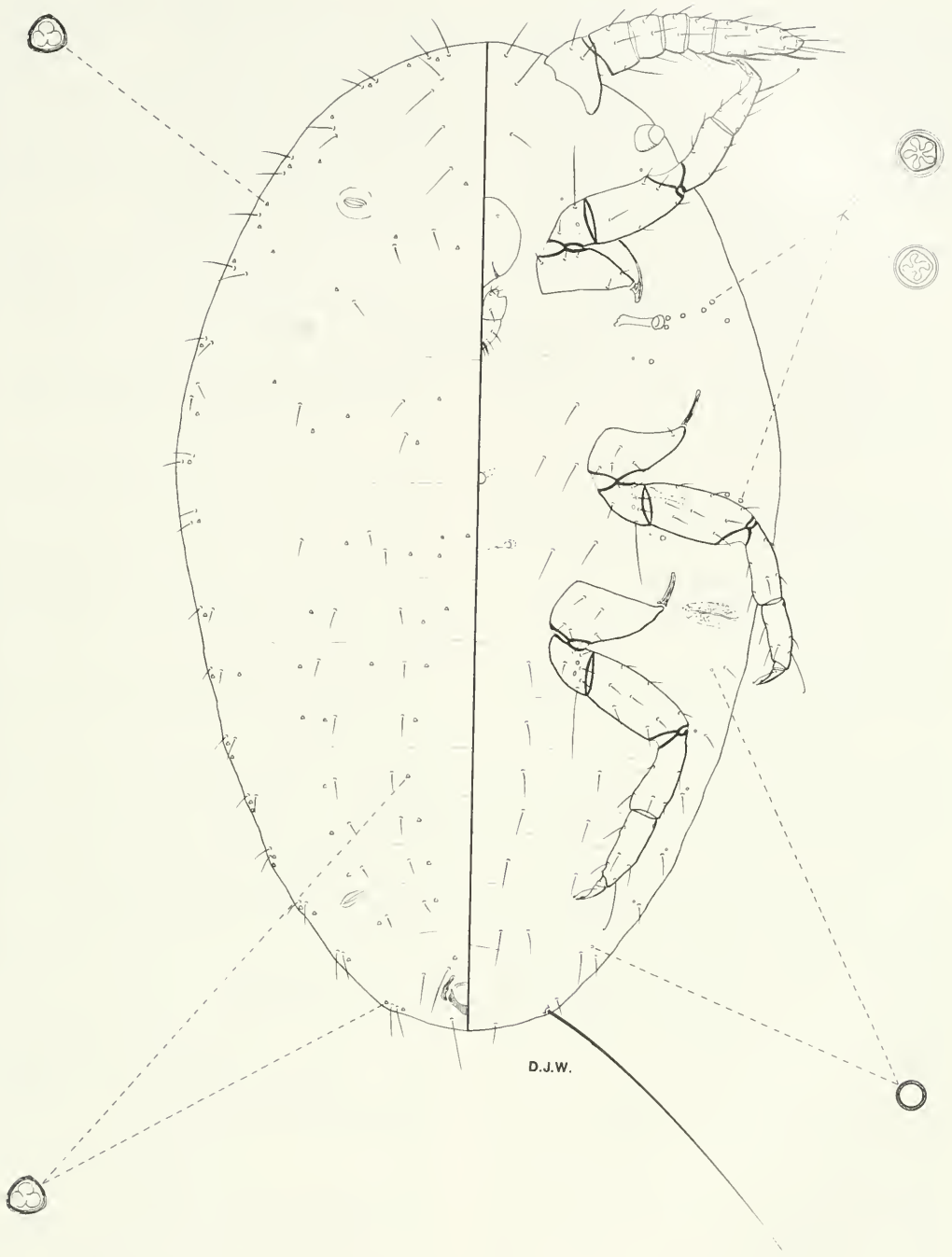

Fig. 8. *Quadrigallicoccus lauracearum.* First instar.

few. Claw with denticle. Pores of trilocular, quadrilocular, and quinquelocular type. Without dermal sclerotization.

Etymology.—The name of this genus is formed from the Latin prefix "*quadr-*" meaning four, "galla" meaning plant swelling or gall, and "*coccum*" meaning seed or scale insect. *Quadrigallicoccus* is a masculine noun and refers to the unusual quadrilocular pores and gall-forming habit that are characteristic of this mealybug.

Notes.—This genus is distinct from all others known to the authors by the presence of quadrilocular pores that have the same swirling pattern as the normal pseudococcid trilocular pore, the gall-forming habit, and the presence of an anal ring that lacks setae and has obliterated pores. The adult male is unique because of the long penial sheath, the heavily sclerotized abdominal sternites and tergites, and the unusual structure of the ventral eyes.

Quadrigallicoccus lauracearum Williams and Miller, new species

Type material.—The holotype adult female is on a slide with 1 other adult female and 4 first instars and is labeled as follows: Left label "COSTA RICA/ Cartago/ Tobosi/ 1700 m/ November 1991/ P. Hanson, coll./ ex. Aiouea/ costaricense, gall;" the right label gives a map of the location of the holotype and states "*Quadrigallicoccus/ lauracearum*/ Williams & Miller/ HOLOTYPE/ & PARATYPE" (USNM). This collection also contains 7 adult females and 24 first instars (USNM). Additional collections are: COSTA RICA, Cartago, Tobosi, 1700 m, April 6, 1992/ P. Hanson and D. Hollis, on *Aiouea costaricense* (Lauraceae) (2 adult females, 7 adult males, 6 second-instar females, 1 second-instar male) (BMNH, USNM); COSTA RICA, Monte Verde Road to San Luis, March 6, 1991, J. Blackmer, on *Nectandra salicina* (Lauraceae) (5 adult females) (BMNH, MNHN, UCD, USNM).

Notes.—The gall is formed from the petiole of the host and is woody.

Etymology.—The species epithet is derived from the Latin genitive plural of the host plant family Lauraceae.

Description.—*Adult female* (Fig. 4): Slide-mounted holotype 2.6 mm long, 2.0 mm wide; paratypes 2.3(1.4–3.0) mm long, 2.0(1.3–2.5) mm wide. Body nearly round, without dermal sclerotization.

Dorsum with trilocular pores abundant over surface. Minute discoidal pores scattered among trilocular pores. Oral-collar tubular ducts about same length as diameter, wider than diameter of trilocular pore, present in small numbers in marginal areas of abdomen. Setae short, in segmental rows; without elongate anal-lobe setae.

Anal ring represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores usually obliterated by heavy sclerotization of ring, occasionally with a few visible; area above anal tube with series of small sclerotized protrusions.

Venter without multilocular pores. Quadrilocular pores most abundant over surface, with swirled pattern like triloculars; quinquelocular pores primarily in area of spiracles, also with swirled pattern. Discoidal pores in large clusters laterad of vulva; minute discoidal pores scattered over surface. Oral-collar tubular ducts restricted to margin of abdomen, uncommon. Longest setae near vulva, in clusters; setae on rest of surface unusually small.

Without circulus. Labium 3-segmented, 161 μ long; paratypes 141(133–149) μ long. Antennae represented by unsegmented sclerotized knob containing 8 setae, paratypes 13(6–17) setae. Legs absent.

Notes: The above description is based on 14 specimens from 2 localities.

Adult male (Fig. 5): Slide-mounted specimen 1.9(1.9–2.0) mm long, 0.5(0.4–0.5) mm wide. Body unusually elongate and narrow, with abdomen constricted and tapering distally.

Dorsum with 1 pair of tail-forming pore clusters; each cluster with 2 elongate setae 356(298–397) μ long and 44(38–52) mul-

tilocular pores; without additional setae or discoidal pores. Multilocular pores uncommon, with 1 or 2 in marginal areas of any or all of segments I to V, with 1 or 2 on each side of head, with 3, 4, or 5 loculi, quadriloculars most abundant. Discoidal pores associated with multiloculars, rarely with 1 or 2 in marginal areas of abdominal segments unassociated with multiloculars. Minute tubular ducts present in clusters along margin of abdomen. Body setae bristle shaped. Abdominal sclerotization present medial and mediolateral areas of segments II or III to segment VIII. Metapostnotal ridge conspicuous. Scutellum rectangular, without scutellar ridge, with several setae. Scutum sclerotized throughout, scutum with several small setae. Prescutum oval, with weakly defined prescutal suture, with short setae. Post tergite present, usually with 1 seta. Pronotal ridges heavily sclerotized. Hamulohalterae 109(96–120) μ long, with 1 apical hooked seta. Mesothoracic wings 1644(1500–1767) μ long, each with 2 or 3 basal setae, discoidal pores difficult to see, when visible with 4 or 5. Dorsal arm of midcranial ridge extending to posterior margin of dorsal eye, not touching lateral arms. Dorsomedial sclerite weakly sclerotized with several setae. Dorsal eye with small depression around lateral margin, with a few small dimples in depression, 36(35–37) μ in diameter. Lateral ocellus 21(15–27) μ in diameter, located at junction of preocular and postocular ridges. Ocular sclerite lightly sclerotized.

Penial sheath 544(533–564) μ long, 56(50–62) μ at its widest; length/width 9.8(9.1–11.0). Aedeagus 497(484–527) μ long, apically acute.

Venter with setae bristle shaped. Multilocular pores absent. Minute tubular ducts present in clusters along margin of abdomen. Abdominal sclerotization conspicuous, present on medial and mediolateral areas of segments II or III to VIII. Prosternal ridge well developed, sternite weakly sclerotized. Preoral ridge weakly developed. Mouth tubercle with 2 setae. Ocular sclerite weakly sclerotized. Ventral midcranial ridge well developed, broad, with lateral arms. Ventral eyes present on conspicuous protrusion, surrounded by trough like depression with sclerotized dimples laterally, 39(35–44) μ in diameter.

Hind femur 218(207–225) μ long; tibia 242(230–254) μ long; hind tarsus 81(77–84) μ long; femur/tibia 0.9; tibia/tarsus 3.0(2.8–3.2). Leg setae bristle shaped; antennae primarily with slightly fleshy setae, usually with 1 to 3 bristle shaped setae on each segment, first segment with bristle-shaped setae only; capitate setae usually absent from antennae, rarely with 1 or 2 such setae present with slightly enlarged club on apical segment. Tarsal digitules capitate; claw digitules acute, less than ¼ length of claw; claw with inconspicuous denticle near tip. Antennae 10-segmented, 965(942–986) μ long; segment 3 longest, 124(119–131) μ long; segment 10, 91(79–99) μ long; segment 3/10 1.4(1.2–1.6).

Notes: The above description is based on 7 specimens from 1 locality.

Second-instar female (Fig. 6): Slide-mounted specimens 0.6(0.5–0.6) mm long, 0.4(0.3–0.4) mm wide. Body oval, without dermal sclerotization.

Dorsum with trilocular pores restricted to single incomplete line along body margin. Minute discoidal pores absent or present in small numbers on body margin of thorax. Oral-collar tubular ducts of 1 size, present in 4 longitudinal lines on each side of body, usually absent on posterior abdominal segments; unusual minute tubular ducts absent. Setae shorter than those on venter, in segmental rows. Dorsal ostioles absent from abdomen, present on head.

Anal ring associated with segment VII, not near apex, represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores concentrated in cluster near anterior end of each side of sclerotization of ring, usually with 2 pores on each side of ring.

Venter without multilocular pores. Other pores primarily of quadrilocular type, also

with triloculars and quinqueloculars, present near spiracles. Minute discoidal pores in single lateral line on each side of abdomen, with 1 pore associated with each spiracle, and 1 or 2 present on each side of posterior end of head. Oral-collar tubular ducts present in lateral line on each side of body. Longest setae near vulva or on segment IV or V, anal-lobe seta 280(235–309) μ long. Sclerotized slit present laterad of hind pair of legs. Eye with anterior extension containing small swelling in addition to main swelling of eye.

Without circulus. Labium 3-segmented, 68(62–74) μ long. Antenna 6-segmented without partially divided segments, 183(173–198) μ long. Legs well developed, hind femur 96(94–99) μ long; hind tibia 67(67–69) μ long; hind tarsus 59(57–62) μ long; hind tibia/tarsus 1.2(1.1–1.2); femur/tibia 1.4(1.4–1.5); tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on 6 specimens from 1 locality.

Second-instar male (Fig. 7): Slide-mounted specimen 1.2 mm long, 0.7 mm wide. Body oval, without dermal sclerotization.

Dorsum with trilocular pores scattered over surface except absent from segments VIII and sometimes VII. Minute discoidal pores scattered among trilocular pores. Oral-collar tubular ducts absent; unusual minute tubular ducts scattered among triloculars. Setae nearly as long as those on venter, in segmental rows. Dorsal ostioles on abdomen and head.

Anal ring near abdominal apex, represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores concentrated in cluster near anterior end of each side of sclerotization of ring.

Venter without multilocular pores. Other pores primarily of quadrilocular type, also with triloculars and quinqueloculars, present near spiracles and on anterior abdominal segment. Minute discoidal pores scattered over surface of anterior abdomen, thorax and posterior thorax except absent from medial areas. Minute tubular ducts present in lateral line on each side of body. Longest setae near vulva, anal-lobe seta about 110 μ long. Sclerotized slit present laterad of mid pair of legs. Eye with anterior extension containing small swelling in addition to main swelling of eye.

Without circulus. Labium 3-segmented, 96 μ long. Antenna 7-segmented with third segment partially divided, 279 μ long. Legs well developed, hind femur 128 μ long; hind tibia 90 μ long; hind tarsus 82 μ long; hind tibia/tarsus 1.1; femur/tibia 1.4; tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on a single specimen.

First instar (gender not determined) (Fig. 8): Slide-mounted paratypes 0.8(0.8–0.9) mm long, 0.5(0.4–0.5) mm wide. Body elongate oval.

Dorsum without cerarii with conical setae; homologous paired setae present along body margin. Trilocular pores arranged in 3 pairs of longitudinal lines, 1 or 2 pores along body margin and associated with 2 setae on each side of segment, 1 pair present in mediolateral lines, 1 pair in submedial area, a few others scattered on thorax and head. Discoidal pores absent. Oral-collar tubular ducts absent. Setae arranged in 3 pairs of longitudinal lines; marginal line composed of 2 setae; mediolateral and submedial lines complete; dorsal body setae unusually elongate; anal-lobe seta 244(222–259) μ long. Ostioles present, anterior pair well developed, posterior pair weakly developed.

Anal ring horseshoe shaped, with 2(1–2) pores on each side of ring; without anal-ring setae.

Venter without trilocular pores present on abdomen; pores near spiracles with 3 to 5 swirled loculi. Discoidal pores present in lateral line with 1 on each side of each abdominal segment; also present posterior of each spiracle and or near posterior margin of head. Oral-collar tubular ducts absent.

Longest setae on posterior abdominal segments; setae arranged in 3 pairs of longitudinal lines, submarginal, mediolateral, and submedial. Slightly sclerotized slit laterad of hind pair of legs.

Without circulus. Labium 77(63–84) μ long. Antenna 6-segmented, often with 6th segment partially divided, 214(198–229) μ long. Legs well developed, hind femur 98(89–101) μ long; hind tibia 71(67–74) μ long; hind tarsus 72(69–74) μ long; tibia/tarsus 1.0(0.9–1.0); femur/tibia 1.4(1.2–1.5); tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on 28 specimens from 1 locality.

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THE GENUS *COSTATRICHIA* MOSELY IN COSTA RICA, WITH A REVIEW OF THE NEOTROPICAL SPECIES (TRICHOPTERA: HYDROPTILIDAE)

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Abstract.—Three new species of *Costatrichia* (Trichoptera: Hydroptilidae) are described from Costa Rica, ***C. carara, C. flinti,*** and ***C. zopilote,*** and one from Venezuela, ***C. cressae.*** The subspecies *Costatrichia tripartita venezuelensis* from Venezuela is elevated to species status and newly recorded from Costa Rica. Illustrations and a key to males of the 12 known species in the genus are provided. The females of *C. carara, C. simplex, C. tripartita,* and *C. zopilote* are illustrated.

Key Words: Trichoptera, Costa Rica, Venezuela, taxonomy, microcaddisflies, Neotropics, key

This paper on the genus *Costatrichia* Mosely represents another in a continuing series of works emphasizing the taxonomy of the microcaddisfly fauna of Costa Rica. In cases where a broader review of the fauna is necessary to resolve taxonomic problems, we have expanded our study beyond Costa Rica, as we have done in this paper. We herein describe four new species, including one from Venezuela, redescribe another four species known from Costa Rica, elevate one subspecies to full species status, and illustrate two species not reported from, but likely to occur in Costa Rica. As well, we have included new figures of *C. noite* Angrisano since we have seen additional material from Peru [Loreto: Sucusari River at Explornapo Camp, 13 January 1993, L. J. Davenport (NMNH, UMSP)], suggesting a wider range for the species than previously suspected. A key is included to separate the males of all known species in the genus.

The genus *Costatrichia* was erected by Mosely in 1937 for *C. lodora* from Chiapas, Mexico. Since then, six additional species have been described, including *C. bipartita* Flint 1970 (Nicaragua), *C. noite* Angrisano 1995 (Uruguay), *C. panamensis* Flint 1967 (Panama), *C. simplex* Flint 1970 (Costa Rica, El Salvador, Honduras, Mexico, Nicaragua), *C. spinifera* Flint 1970 (Panama), and *C. tripartita* Flint 1970 (Panama). In addition, Flint (1981) also described the subspecies *C. tripartita venezuelensis* from Venezuela. Flint (1970) recorded *C. lodora* and *C. simplex* from Costa Rica. Another of these species, *C. spinifera* Flint from Panama, is herein recorded from Costa Rica. With the description of four new Costa Rican and Venezuelan species in this paper and the elevation of the subspecies to full specific status, 12 species are now known in the genus. The immature stages of *Costatrichia* are unknown and nothing of substance is known about the biology of the genus except that adults are usually taken near flowing water.

Flint (1970) separated the genus into two groups based on features of the male geni-

talia, head and wings. The *simplex* group contained those males with unmodified antennae, and no basal costal bulla in the forewing, while the *lodora* group contained those species with modified antennae, a costal bulla, and divided inferior appendages. Flint (1970) mentioned the close similarity among *Costatrichia, Leucotrichia,* and *Zumatrichia,* with greater similarity to the latter genus. In Marshall's (1979) key the *lodora* group keyed close to *Acostatrichia* Mosely and the *simplex* group keyed separately with *Betrichia argentinica* Flint, *Leucotrichia malleopicta* group, and *Celaenotrichia* Mosely. It may be, however, that *Costatrichia* is paraphyletic, with the *simplex* group belonging to another genus. Costal bullae and modified male antennae occur in other genera within the Leucotrichiini. As mentioned by Marshall (1979) and Flint (1992), the generic limits of those taxa placed in the Leucotrichiini, including *Costatrichia,* are not clearly defined. Only a reassessment of all genera in the tribe will resolve the taxonomic problems. We have recently finished a review of the Stactobiini which necessitated an examination of the Leucotrichiini. A complete reassessment of the Leucotrichiini is beyond the scope of this paper, but we are pursuing these studies. In anticipation of this larger assessment and for ongoing research in biodiversity conservation and aquatic ecology, we take this opportunity to provide names for these new species now. However, until the larger assessment of the leucotrichiine genera and their characters occurs, the exact placement or status of the genus *Costatrichia* remains in question.

Types of species described in this paper are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CMNH), the Universidad Central de Venezuela, Maracay (UCV), and the Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica (INBIO) as noted in the descriptions. Morphological descriptions follow the terminology of Marshall (1979). Specimen length is measured from the tip of the wings to the top of the head and is given as a range when more than one specimen was measured.

Costatrichia Mosely

Costatrichia Mosely 1937: 166 [Type species: *Costatrichia lodora* Mosely 1937, original designation].—Flint 1970:11 [revision].

Costatrichia is defined by the following characteristics: Head unmodified in males and females; 3 ocelli in males and females, antenna with scape elongate in most males, otherwise basal segments unmodified, remaining segments terete, or with middle segments broad in males of some species; males usually with costal bulla on forewing, comprised of short thickened setae, varying in length; transverse suture on mesoscutellum, metascutellum subpentagonal to triangular in shape; tibial spur formula 1,3,4. Generally brown in coloration with greenish bands or patches of hairs on the forewing. Male genitalia with abdominal segment VII bearing elongate sternal process; segment VIII typically narrowing ventrolaterally; segment IX greatly reduced ventrally, often bearing elongate lateral process and with setose lateral process; segment X short and membranous, partly fused with IX anteriorly. Inferior appendages elongate and conspicuous or absent; subgenital plate present or absent. Phallus with median complex, which includes a basal loop and dorsal window, anteriorly with spines or sclerites. Female genitalia with abdominal segment VII with short sternal process. Segment VIII usually with patches of short spicules. Bursa copulatrix with lyrelike vaginal sclerite bearing teeth on inner margin.

Costatrichia lodora Mosely
(Figs. 1A, 2A, 3, 4)

Costatrichia lodora Mosely 1937:168.

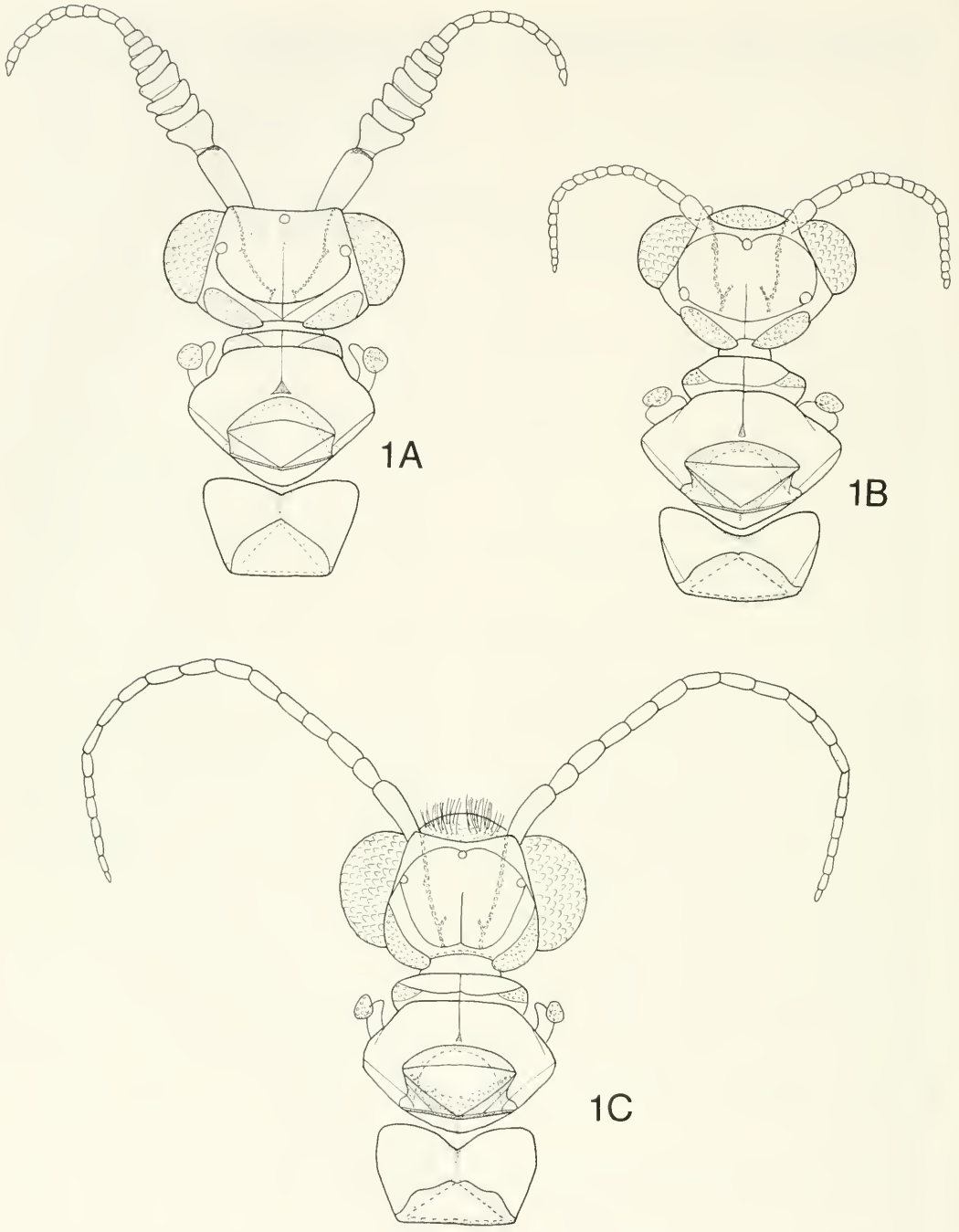
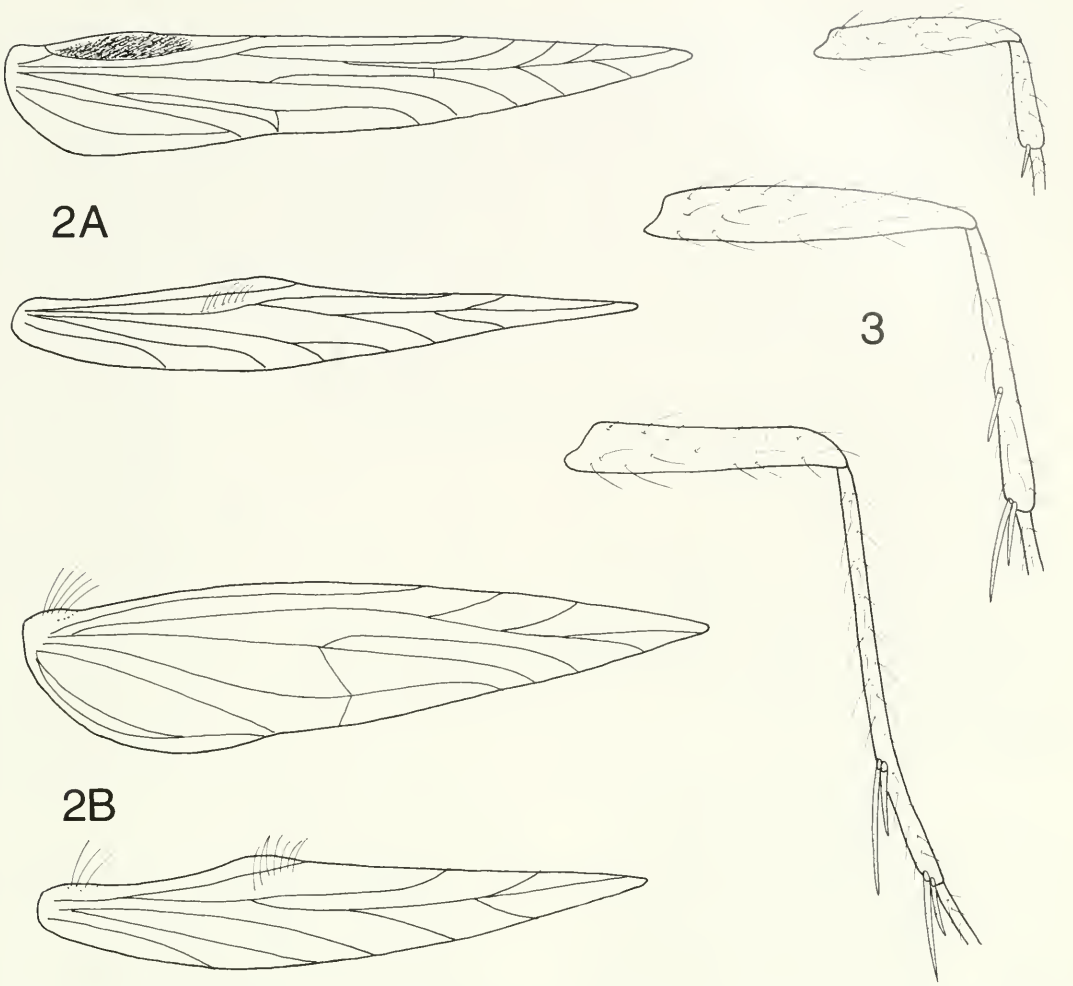


Fig. 1. Head and thorax of male *Costatrichia*, dorsal view. A, *C. lodora*. B, *C. spinifera*. C, *C. zopilote*.



Figs. 2–3. 2, Fore and hind wings of *Costatrichia*. A, *C. lodora*. B, *C. zopilote*. 3, Fore, mid and hindlegs of *C. lodora*.

Costatrichia lodora is most similar to the following new species. Both are related to *C. panamensis*, differing primarily in the shorter, more rounded posterior process from abdominal segment VIII.

Male.—Length 3.4–4.2 mm. Brown in alcohol. Antenna with 19 segments, scape elongate, basal flagellar segments broad; 3 ocelli. Forewing with elongate costal bulla. Abdominal sternum VII with elongate, slender process. Segment VIII narrowing posterolaterally to acute point; in ventral aspect with narrow posteromesal excision. Segment IX mostly within segment VIII, narrowing anteriorly, posteriorly with small dorsal knob and elongate posteroventral process, dorsolaterally with short setose process; in dorsal view posteroventral process generally truncate, slightly emarginate posteriorly. Segment X membranous; in dorsal view, triangular posteriorly, broadly fused to segment IX anteriorly. Inferior appendages incised on posterior margin, dorsal arm thin and slightly narrowing posteriorly, ventral arm broadly rounded; in ventral view rectanguloid with apices curved slightly inward, thin lateral sclerotized processes sharply curved inward at apex. Phal-

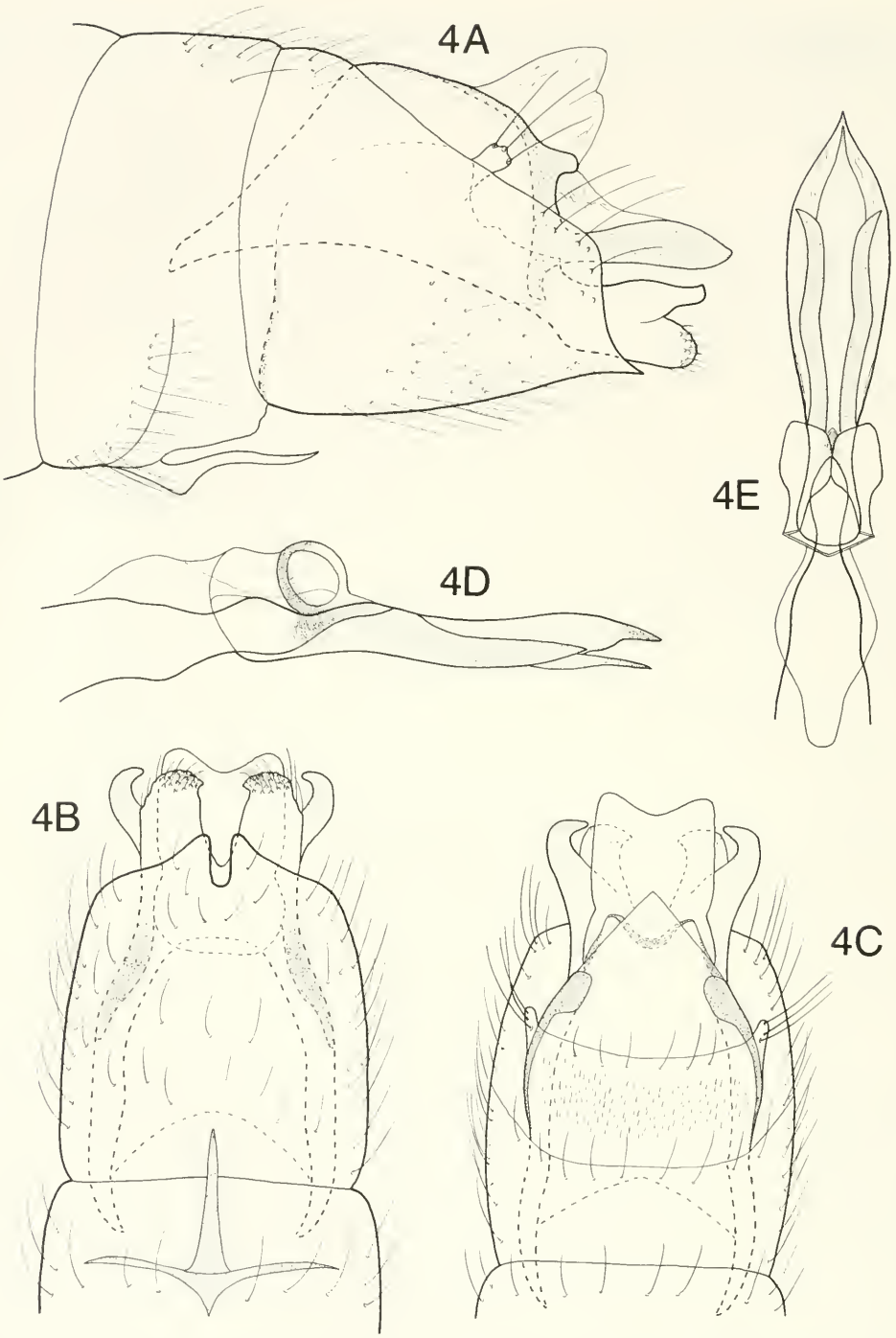


Fig. 4. *Costatrichia lodora*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

lus tubular basally with midlength complex bearing dorsal loop, apically with pair of elongate, thin lateral sclerites and middle plate narrowing to apical point.

Female.—Unknown.

Material examined.—COSTA RICA: Alajuela: Rio Pizote, ca 5 km N Dos Rios, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth, 1 ♂ (UMSP); Finca El Ensayo, Cerro Campana, iv.1994, F. Muñoz, 1♂ (UMSP); Quebrada Arena, Puesto San Ramón, iv.1994, F. Muñoz, 1♂ (UMSP). Guanacaste: Río Tizate, 2 km NE Cañas Dulces, 10.773°N, 85.449°W, el. 275 m, 28.vi.1986, Holzenthal, Heyn, Armitage, 2 ♂ (INBIO); Parque Nacional Guanacaste, El Hacha, Quebrada Alcornoque, 11.009°N, 85.577°W, el. 250 m, 26.vii.1987, Holzenthal, Morse, Clausen, 1 ♂ (UMSP). Heredia: Río Bijagual on road to Magsasay, 10.408°N, 84.076°W, el. 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 5 ♂ (UMSP). BELIZE: Stan Creek District: Cockscomb Wildlife Preserve, Maya Mountains, Cockscomb-B4, 16.80°N, 88.55°W, el. 200 m, 10–11.v.1990, Adams and Dow, 1 ♂ (CMNH).

Comments.—The specimen of *C. lodora* recorded from San José, Costa Rica, Río General, Pacuare, by Flint (1970) belongs to a new species, *C. flinti,* described below. Flint (1970) noted several differences when the specimen was compared to a paratype of *C. lodora,* but, with insufficient material, these differences were attributed to intraspecific variation.

Costatrichia flinti, Holzenthal and Harris, new species

(Fig. 5)

Costatrichia lodora Flint 1970: 12 [paratype from Río General, Pacuare, Costa Rica], *nec* Mosely 1937.

This species is very similar to *C. lodora* Mosely differing in the shape of the inferior appendages, which have a broad dorsal arm, and in the wide lateral sclerites of the phallus.

Male.—Length 3.3–4.3 mm. Brown in alcohol. Antenna with 19 segments, scape elongate, basal flagellar segments broad; 3 ocelli. Forewing with elongate costal bulla. Abdominal sternum VII with slender elongate process. Segment VIII narrowing posterolaterally to elongate, narrow spine; in ventral view narrowing posteriorly with small mesal incision. Segment IX narrowing anteriorly, posteriorly with small dorsal process and elongate posteroventral process, laterally with short setose process; in ventral view, posteroventral process generally truncate, slightly emarginate posteriorly. Segment X membranous; in dorsal view triangular posteriorly, broadly fused to segment IX anteriorly. Inferior appendages broadly incised on posterior margin, broad dorsal arm about twice as wide as narrow ventral arm; in ventral view with basomesal shelves which curve inward, distally narrowing to acute apices. Phallus tubular basally, with midlength complex bearing dorsal loop, apically with wide lateral sclerites which narrow to acute distal points, middle plate narrowing to apical point.

Female.—Unknown.

Type material.—Holotype, ♂. COSTA RICA: Puntarenas: Río Singrí, ca 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal, Morse, Fasth, (NMNH). Paratypes: COSTA RICA: Puntarenas: same data as holotype, 3 ♂ (INBIO), 9 ♂ (UMSP); Quebrada Potrero near Potrero Grande, 5.vii.1992, T. Shepard, 3 ♂ (INBIO), 15 ♂ (UMSP); Río Plantanar, Salitre, 6.5 km E Buenos Aires, el. 455 m, 8–9.vi.1992, F. Muñoz, 2 ♂ (NMNH), 20 ♂ (UMSP). San José: Río General, Pacuare, 1.vii.1967, P. J. Spangler, 1 ♂ (NMNH).

Etymology.—Named for Dr. Oliver S. Flint, Jr. who first recognized the differences between the new species and the closely related *C. lodora.*

Costatrichia simplex Flint

(Figs. 6–7)

Costatrichia simplex Flint 1970: 13.

Males of *Costatrichia simplex* are most similar to *C. spinifera* in the presence of

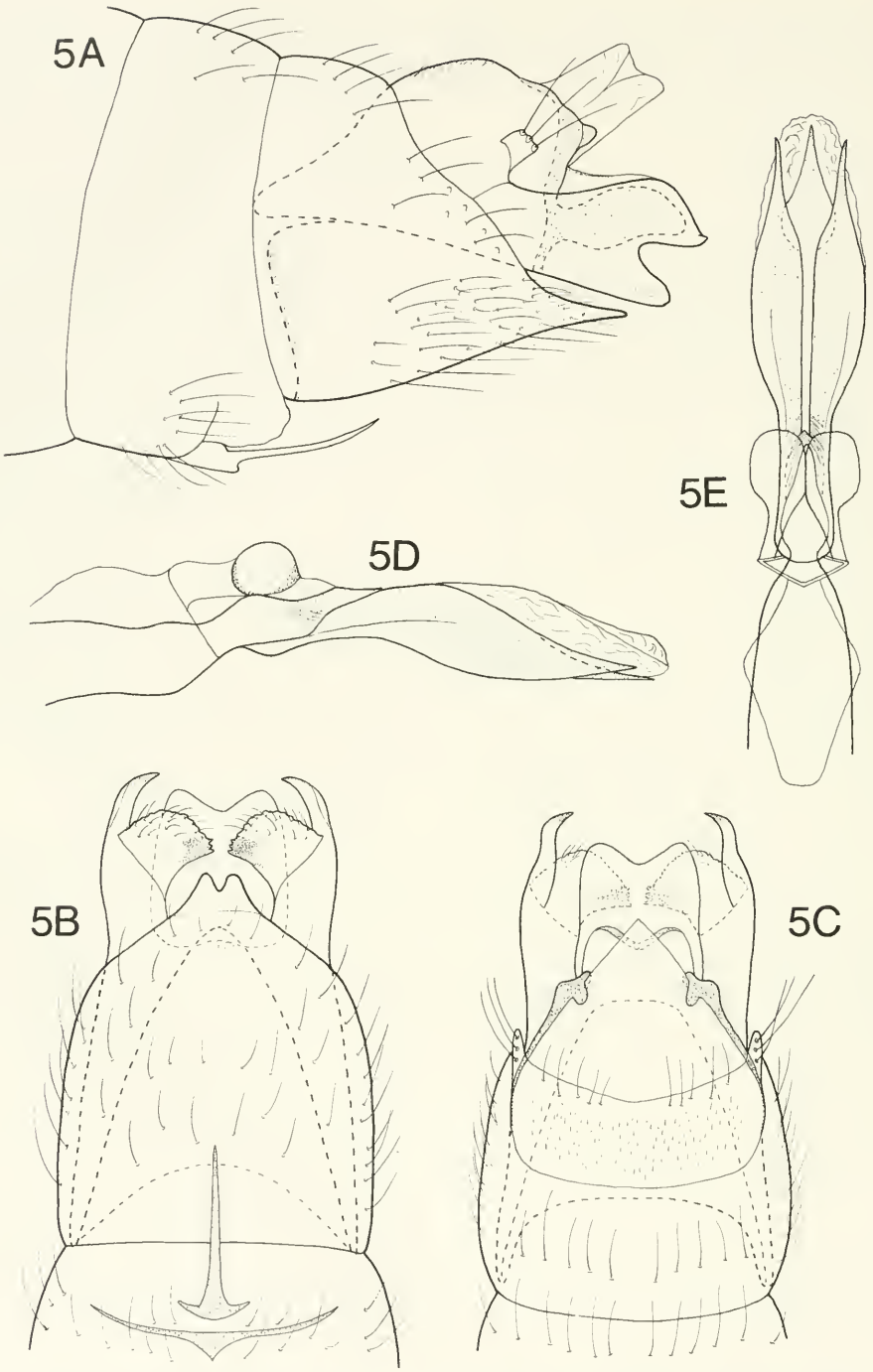


Fig. 5. *Costatrichia flinti*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

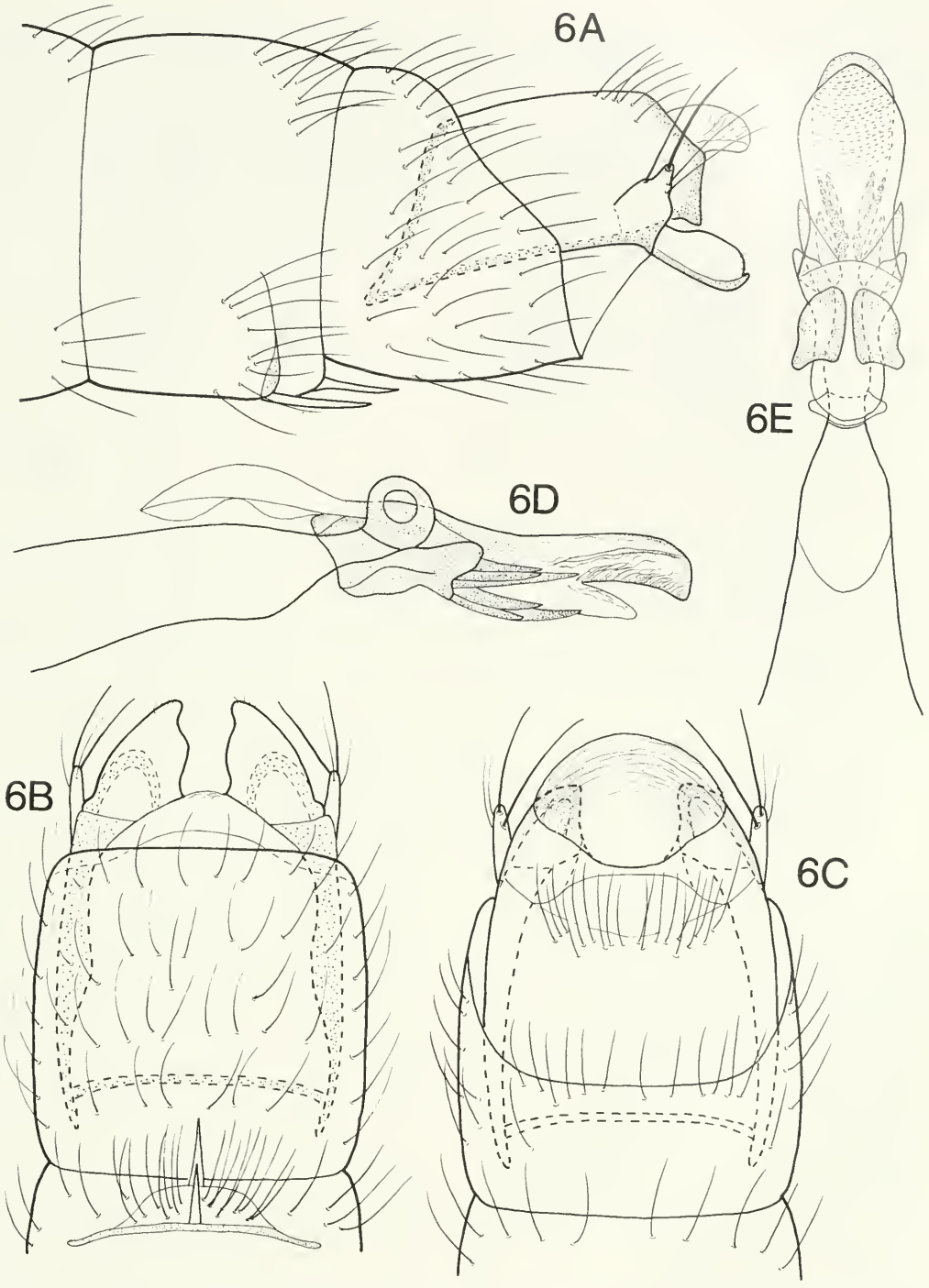
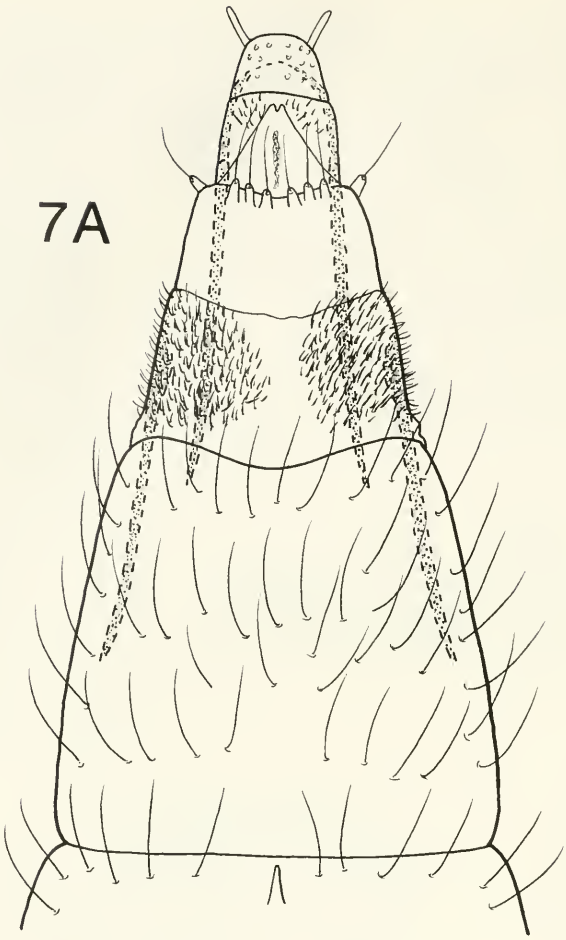
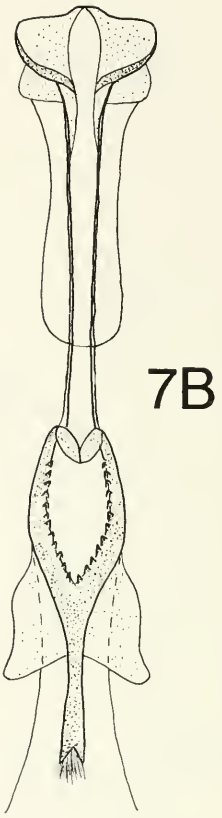


Fig. 6. *Costatrichia simplex*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.





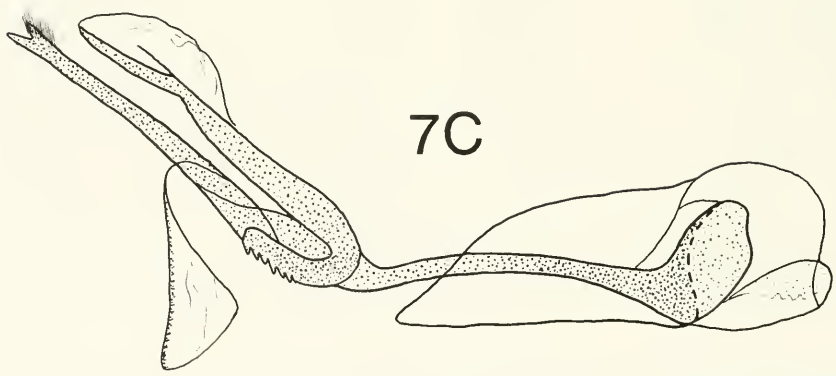


Fig. 7. *Costatrichia simplex*, female genitalia. A, Terminal abdominal segments, ventral. B, Bursa copulatrix, ventral. C, Bursa copulatrix, lateral.

numerous phallic spines. The two species are easily separated by the absence of posterior spines from segment VIII in *C. simplex*. Since females of only a few *Costatrichia* are known, determining affinities is difficult. Females of *C. simplex* differ from those of the *tripartita* group by the narrow posterior portion of the bursa copulatrix and lack of lateral membranous folds. The species has been recorded from Costa Rica, El Salvador, Honduras and Mexico.

Male.—Length 4.2–4.6 mm. Head with whitish hair; antenna with 19 segments, terete; 3 ocelli. Forewing mostly brown with narrow greenish stripe at midlength, with greenish area subapically and along posterior margin, costal bulla present, but small and inconspicuous. Abdominal sternum VII with pair of short mesal processes. Segment VIII tapering posteroventrally, truncate in ventral view. Segment IX compressed dorsolaterally, narrowing anteroventrally, obliquely truncate posteriorly, bearing a large setose lobe posterolaterally; in ventral view slightly rounded posteriorly. Segment X membranous, a short round lobe in lateral view; in dorsal view rounded posteriorly, broadly fused to segment IX anteriorly. Inferior appendages rectanguloid, ventral margin sclerotized and extending posteriorly as small lobe; in ventral view triangular, with inner margins sinuate. Phallus tubular basally, with midlength complex bearing dorsal loop, apically with cluster of short spines basally, apex with rings of small spicules; in lateral view, spinal cluster ventrolateral in position.

Female.—Length 3.8–4.4 mm. Coloration as in male. Antenna simple, with 19 segments; 3 ocelli. Forewing without costal bulla. Abdominal segment VI with short sternal process. Segment VII nearly square, slightly emarginate on posterior margin. Segment VIII with patches of short spicules, posterior margin with ring of elongate setae; lateral apodemes extending midway through segment VIII. Segment IX with triangular ventral lobe; lateral apodemes extending through segment VIII. Segment X short, rounded posteriorly bearing pair of apical papillae. Burse copulatrix in ventral aspect thin and elongate; vaginal sclerite lyrelike, with inner margin serrate, connected by thin tube to oval posterior sclerite; in lateral view vaginal sclerite with serrate teeth posteroventrally, bifid anteriorly with cluster of hairs, connected by narrow tube to membranous posterior lobes.

Material examined.—EL SALVADOR: San Salvador, Lake Ilopango near Apulo, 5.viii.1967, Flint and Ortiz, 2 ♂, 3 ♀ paratypes (NMNH). COSTA RICA: Guanacaste: Parque Nacional Santa Rosa, Quebrada San Emilio, 10.862°N, 85.610°W, el. 300 m, 27.vi.1986, Holzenthal, Heyn, Armitage, 1 ♂ (UMSP). NICARAGUA: Solentiname, Isla La Venada, 22.ii.1995, F. Collantes, 2 ♂, 1 ♀ (NMNH).

Comments.—Previously recorded from Costa Rica by Flint (1970): Guanacaste: Río Ahogados, 10 miles northwest of Liberia, 25.vii.1965, P. J. Spangler, 1 ♂ (NMNH); Las Canas, 13.vii.1965, 1 ♂ (NMNH).

Costatrichia tripartita Flint
(Figs. 8–9)

Costatrichia tripartita Flint 1970: 13.

Costatrichia tripartita and the two new species which follow, along with the redefined species *C. venezuelensis*, form a distinct group recognizable by the tripartite inferior appendages. *Costatrichia tripartita* is separated from the rest of the group by the deep mesal incision of the posterior margin of the eighth sternum and the internal spinelike process of this segment. As well, the phallus of *C. tripartita* has a pair of short, acute posterolateral spines. The species is known from Panama, but as we have females from Costa Rica which appear to match females collected with males of *C. tripartita* from Panama, we are here recording the species from Costa Rica. This record from San José remains tentative, however, since females of all *Costatrichia* species are not yet associated and species spe-

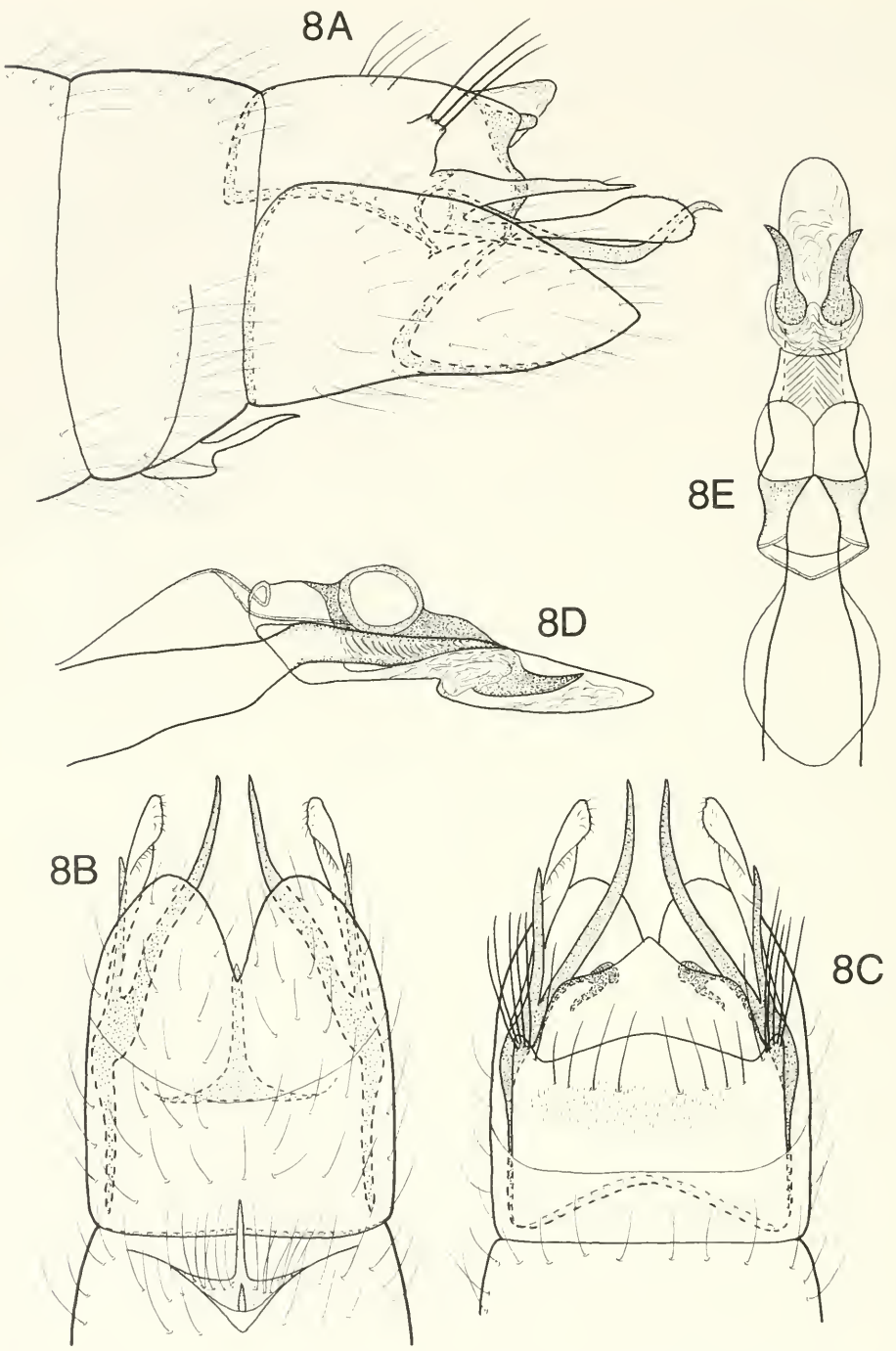


Fig. 8. *Costatrichia tripartita*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

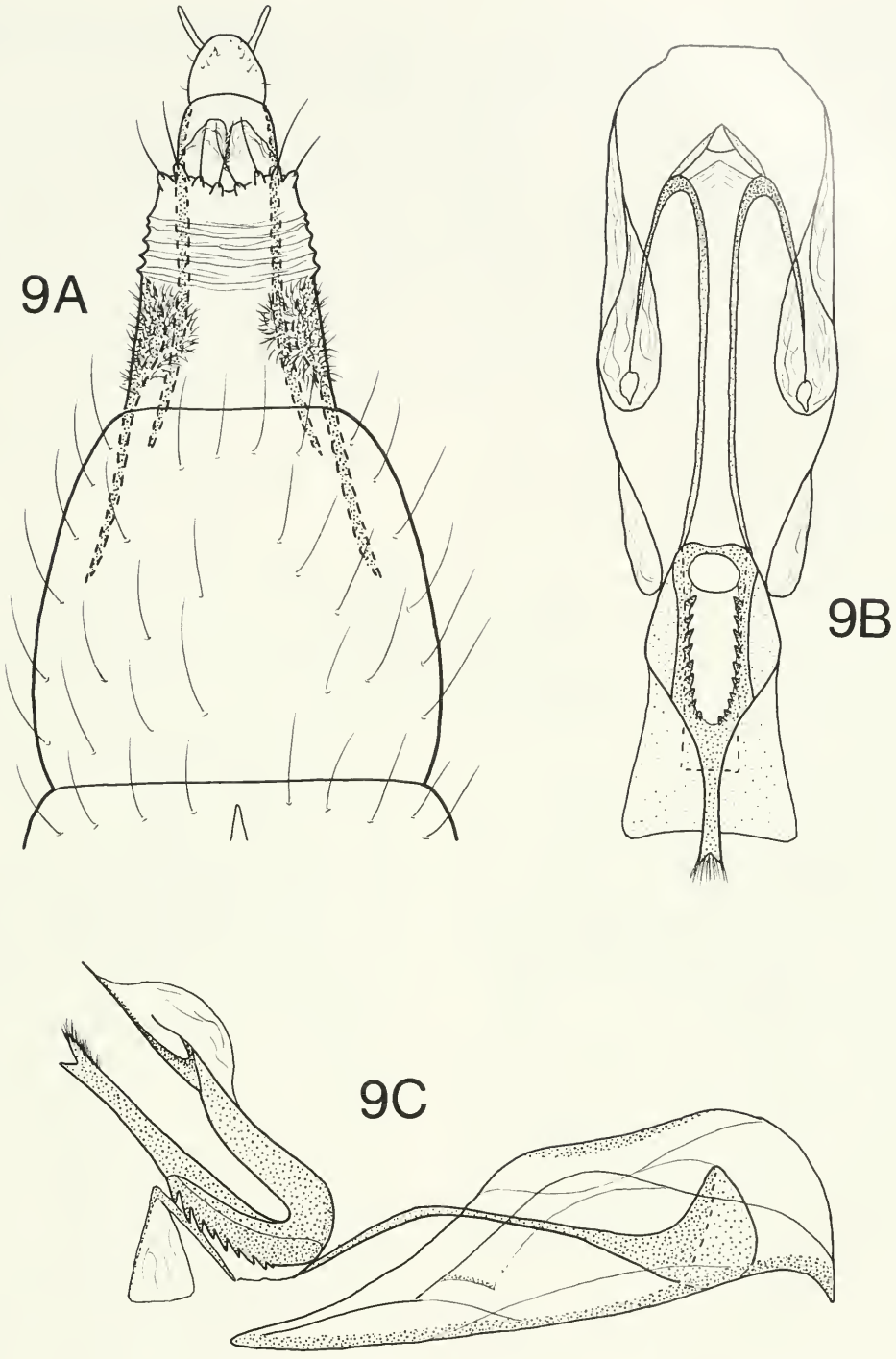


Fig. 9. *Costatrichia tripartita*, female genitalia. A, Terminal abdominal segments, ventral. B, Bursa copulatrix, ventral. C, Bursa copulatrix, lateral.

cific characters are tentative at best. Females of *C. tripartita* differ from the similar *C. carara* and *C. cressae* in the lack of sclerotization in the mesal portion of the bursa copulatrix.

Male.—Length 2.5–3.0 mm. Brown in alcohol. Antenna with 19 segments, scape elongate, basal flagellar segments broad, 3 ocelli. Forewing with elongate costal bulla. Abdominal segment VII narrowing posteriorly to angular apex; in ventral view, deeply incised on posterior margin, internally with mesal spine which connects dorsally with posteroventral margin of segment IX. Segment IX truncate anteriorly and posteriorly, knoblike process posterodorsally, laterally with setal-bearing lobe; rectanguloid in dorsal view. Segment X short and membranous; in dorsal view narrow with mesal extension. Inferior appendages divided into three elongate processes, dorsalmost process thin and elongate, ventralmost process elongate and clublike, mesal process thin, nearly twice as long as dorsal process; in ventral view ventralmost process widening distally to clublike apex, lateral process thin and short, mesal process elongate and curving inward. Phallus wide basally, narrow at midlength complex which bears sclerotized dorsal window and basal loop, laterally with acute posteror spine; in dorsal view with posterior lateral spines, acute apically and slightly diverging.

Female.—Length 2.6–3.1 mm. Brown in alcohol. Antenna simple with 19 segments; 3 ocelli. Forewing without costal bulla. Abdominal sternum VI with short posteromesal process. Segment VII annular. Segment VIII rectangular, with patches of short spicules, posterior margin with ring of elongate setae; lateral apodemes extending through segment VIII. Segment X short, rounded apically, bearing pair of lateral papillae. Bursa copulatrix in ventral view membranous and oval posteriorly, vaginal sclerite rectangular with inner lyrelike structure bearing teeth on inner margin, connected by thin tubes posteriorly; in lateral view vaginal sclerite with serrate teeth posteroventrally, bifid anteriorly with cluster of hairs, connected by narrow tube to membranous posterior lobes.

Material examined.—PANAMA: San Blas: Qda. Pingadi, 9 km N Nusagandi, 1–2.iii.1985, Flint and Louton, 8 ♂, 12 ♀ (NMNH); Río Carti Grande, 2 km W Nusagandi, 5.iii.1985, Flint and Louton, 2 ♂ (NMNH). COSTA RICA: San José: Reserva Biológica Carara, Río del Sur, 1.5 km (rd) S Carara, 9.769°N, 84.531°W, 13.iii.1991, el. 160 m, Holzenthal, Muñoz, Huisman, 27 ♀ (UMSP).

Costatrichia carara, Holzenthal and Harris, new species

(Figs. 10–11)

This is the second species of the *tripartita* group, with greatest similarity to *C. venezuelensis,* new status. Both have the eighth abdominal segment tapering to posterior spines and a similar phallic structure. *Costatrichia carara* is separated by a series of small internal spines from the venter of segment VIII and the short dorsalmost process of the inferior appendage.

Male.—Length 2.6–2.8 mm. Brown in alcohol. Antenna with 19 segments, scape elongate, basal flagellar segments broad; 3 ocelli. Forewing with costal bulla. Abdominal sternum VII with elongate posteromesal process. Segment VIII narrowing posterolaterally to thin, elongate spine; in ventral view tapering posteriorly to pair of mesal horns, series of short internal spines laterally and anterior to mesal horns. Segment IX reduced ventrally, dorsolaterally with seta bearing knob. Segment X short and membranous; in dorsal view rounded posteriorly. Inferior appendages tripartite, divided into pair of lateral processes, ventralmost elongate and clublike, dorsalmost very short, and mesal process thin and elongate; in ventral view ventralmost process narrow, curving inward apically, lateral process very short, inner process elongate and sinuate. Phallus wide basally, narrow at midlength complex, which bears sclerotized

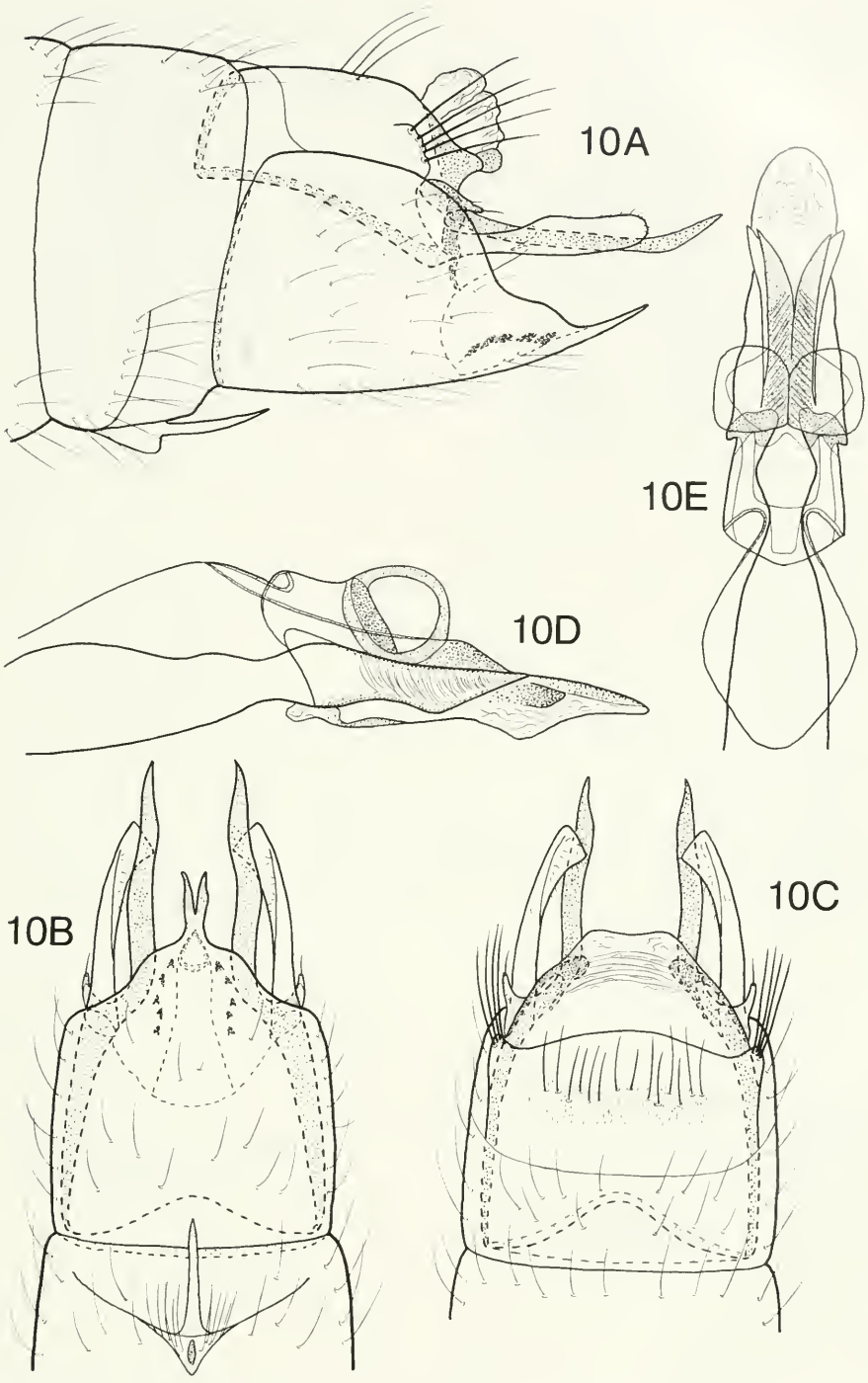


Fig. 10. *Costatrichia carara*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

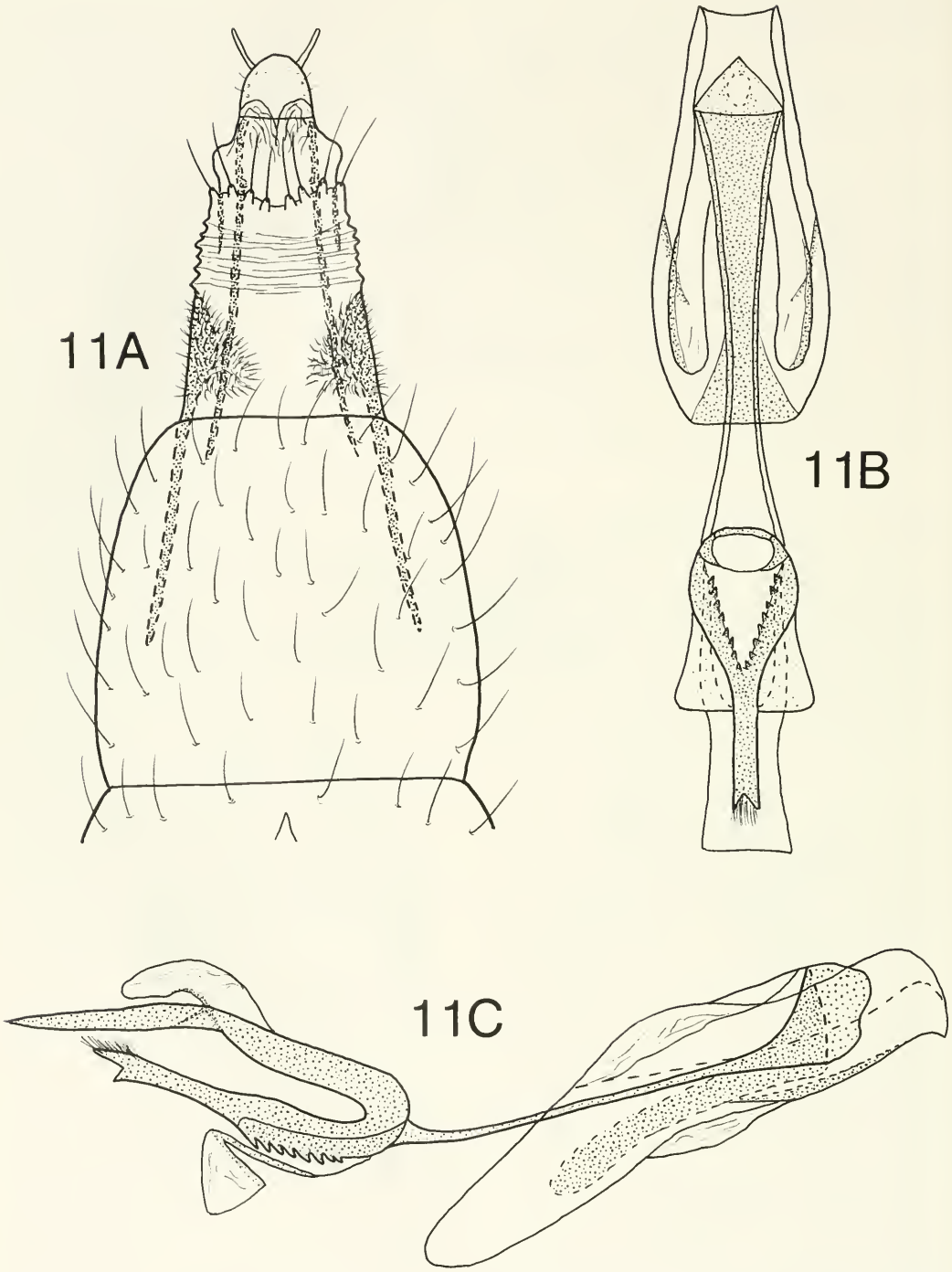


Fig. 11. *Costatrichia carara*, female genitalia. A, Terminal abdominal segments, ventral. B, Bursa copulatrix, ventral. C, Bursa copulatrix, lateral.

dorsal window and basal loop, apically with pair of lateral sclerites.

Female.—Length 2.6–2.8 mm. Brown in alcohol. Antenna simple, terete; 3 ocelli. Forewing without costal bulla. Abdominal segment VI with short sternal process. Segment VII annular. Segment VIII with patches of short spicules, posterior margin with ring of elongate setae; lateral apodemes extending midway through segment VII. Segment IX short with ventral lobes, lateral apodemes extending into segment VII. Segment X short, rounded apically, bearing pair of lateral papillae. Bursa copulatrix in ventral view with oval posterior lobes, rectangular sclerite mesally connected to lyrelike vaginal sclerite by narrow tubes; in lateral view vaginal sclerite with serrate teeth posteroventrally, bifid anteriorly with cluster of hairs, connected by narrow tube to membranous posterior lobes.

Type material.—Holotype, ♂. COSTA RICA: San José: Reserva Biológica Carara, Río del Sur, 1.5 km (rd) S Carara, 9.769°N, 84.531°W, el. 160 m, 13.iii.1991, Holzenthal, Muñoz, Huisman (NMNH). Paratypes: same data as holotype, 1 ♀ (NMNH), 1 ♂, 2 ♀ (UMSP); Reserva Biológica Carara, Quebrada Bonita, 9.775°N, 84.605°W, el. 35 m, 20.v.1990, Holzenthal and Blahnik, 1 ♂ (UMSP).

Etymology.—Named for the Carara Biological Reserve along the south Pacific coast of Costa Rica where the species occurs.

Costatrichia cressae, Holzenthal and Harris, new species

(Figs. 12–13)

This member of the *tripartita* group is most similar to *C. tripartita*. The structure of the phallus is similar in both species, although the posterior lateral processes of *C. tripartita* are acute, rather than rounded as in *C. cressae*. The new species is most readily identified by the presence of a pair of lateral spines on the inner surface of the sternum of segment VIII. The females of both *C. cressae* and *C. carara* have the mesal portion of the bursa copulatrix sclerotized, but this area in *C. cressae* is much wider than in *C. carara*.

Male.—Length 2.5–3.0 mm. Head with whitish hairs; antenna with 19 segments, scape elongate, basal flagellar segments broad; 3 ocelli. Forewings mostly brown with whitish hairs along major veins and at tips; costal bulla present. Abdominal sternum VII with elongate posteromesal process. Segment VIII narrowing posterolaterally to rounded apex; in ventral view emarginate posteriorly, pair of internal lateral spines posteriorly. Segment IX reduced ventrally, dorsolaterally with seta-bearing knob. Segment X short and membranous; in dorsal view truncate posteriorly. Inferior appendages tripartite, divided into pair of lateral processes, ventralmost elongate and clublike, dorsalmost short, fingerlike, mesal process thin and elongate, upturned distally; in ventral view ventralmost process spatulate distally and converging, lateral process short and fingerlike, mesal process thin, sinuate. Phallus wide basally, narrow at midlength complex which bears scelotized dorsal window and basal loop, apically with pair of short lateral sclerites which are rounded posteriorly.

Female.—Length 2.5–3.1 mm. Antenna simple with 19 segments; 3 ocelli. Forewing without costal bulla. Coloration as in male. Abdominal segment VI with short sternal process. Segment VII annular. Segment VIII with patches of short spicules, posterior margin with ring of elongate setae; lateral apodemes extending through segment VII. Segment IX short with ventral lobes, lateral apodemes extending through segment VIII. Segment X short, rounded apically, pair of lateral papillae. Bursa copulatrix in ventral view with oval posterior lobes, large mesal sclerite, connected to lyrelike vaginal sclerite by thin tubes; in lateral view vaginal sclerite with serrate teeth posteroventrally, bifid anteriorly with cluster of hairs, connected by narrow tube to

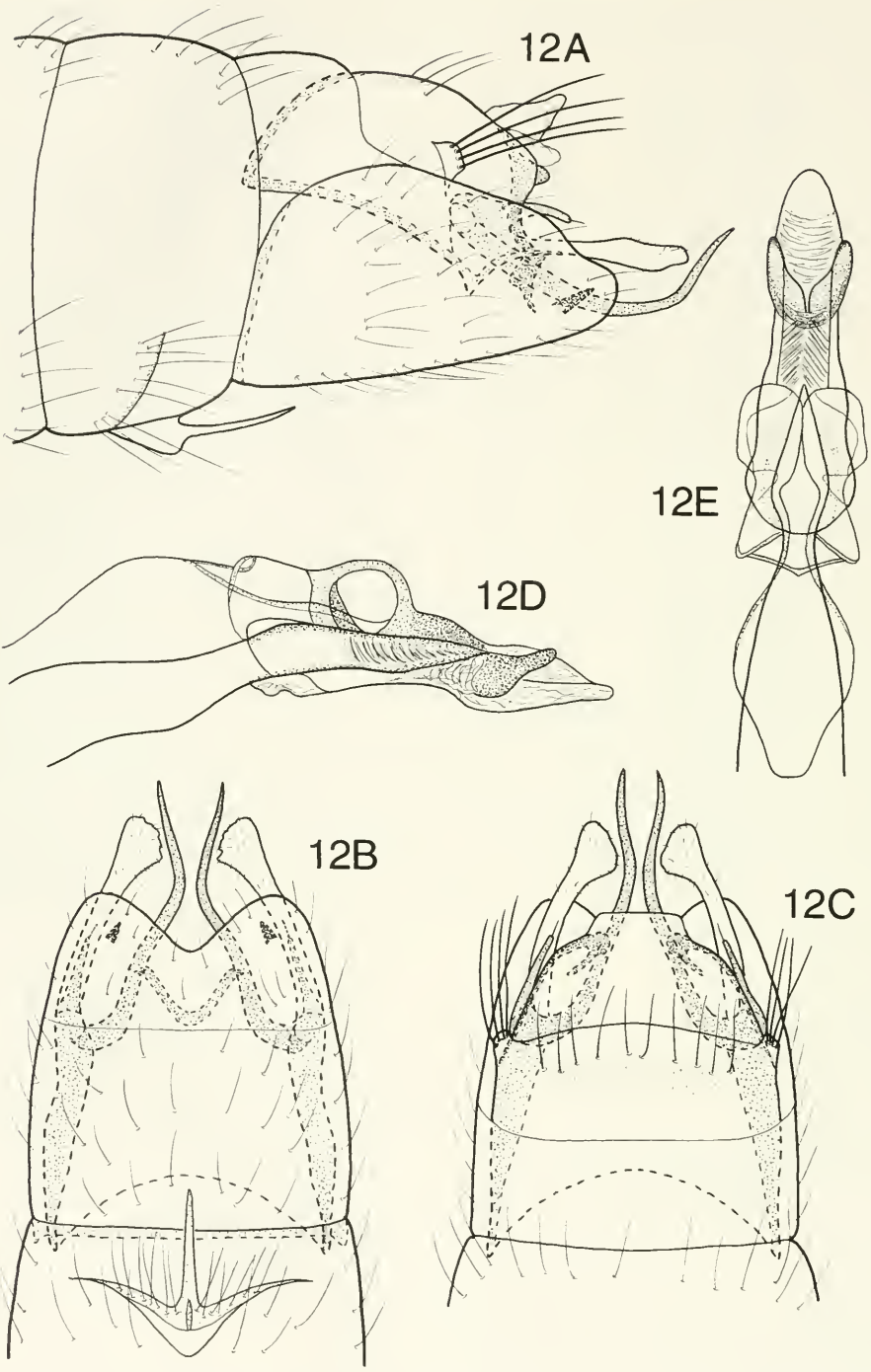
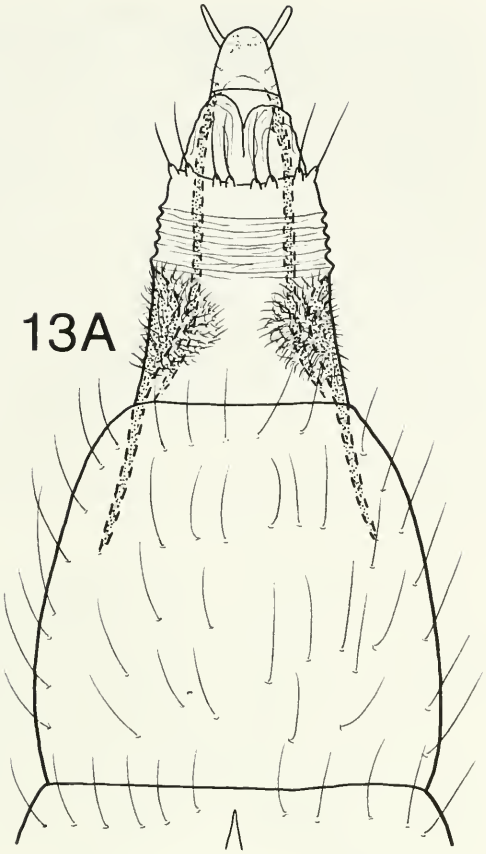
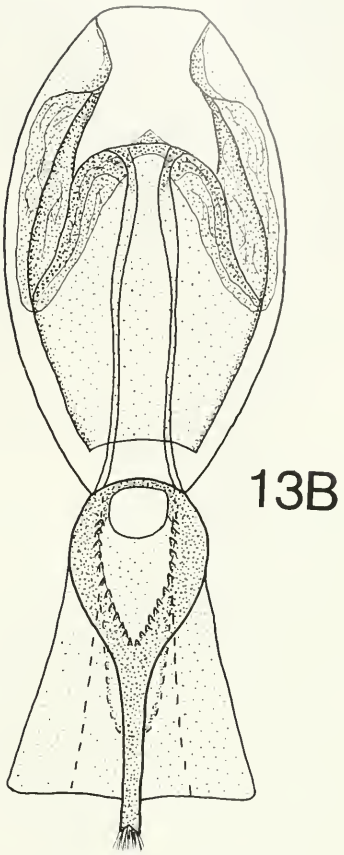


Fig. 12. *Costatrichia cressae*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.





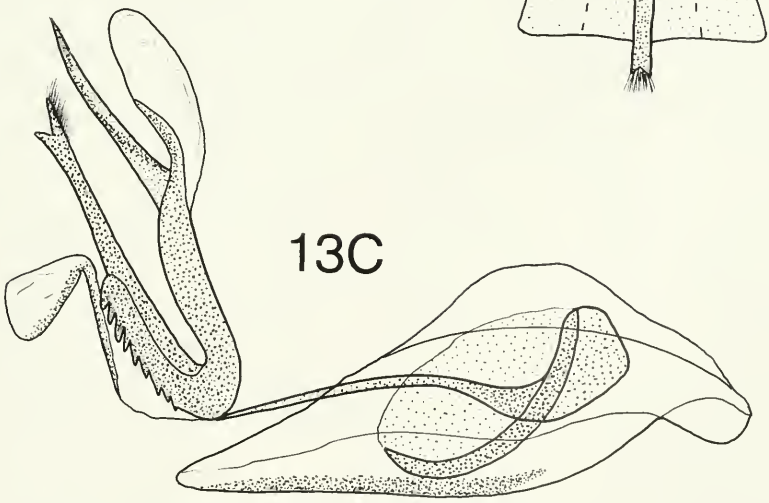


Fig. 13. *Costatrichia cressae*, female genitalia. A, Terminal abdominal segments, ventral. B, Bursa copulatrix, ventral. C, Bursa copulatrix, lateral.

membranous posterior lobes which have a transverse sclerite.

Type material.—Holotype, ♂. VENEZUELA: Distrito Federal, Río Camuri Grande, 1 km S Camuri (nucleo U.S.B.), 10.616°N, 66.175°W, el. 30 m, 24.i.1994, Holzenthal, Cressa, Rincón (NMNH). Paratypes: same data as holotype, 1 ♂ (UCV), 4 ♂, 1 ♀ (UMSP); Aragua State, Parque Nat. Henri Pittier, Río La Trilla, 22.5 km N Rancho Grande on road, 17–19.ix.1979, H. Savage, 3 ♂ (NMNH).

Etymology.—Named for Professor Claudia Cressa, Universidad Central de Venezuela, in recognition of her contributions to Neotropical aquatic insect ecology.

Costatrichia venezuelensis Flint, new status

(Figs. 14–15)

Costatrichia tripartita venezuelensis Flint 1981: 25.

This species was originally described by Flint (1981) as a subspecies of *Costatrichia tripartita.* With the description of several new species in this paper, all similar to *C. tripartita* in the structure of the male genitalia and the discovery of additional material from Costa Rica, the subspecific status of *C. tripartita venezuelensis* was reexamined. The subspecies differs from *C. tripartita* in the appearance of abdominal sternum VIII, which lacks the prominent emargination on the posterior margin. In *C. tripartita venezuelensis* the sternum is truncate or tapering and terminates in a pair of mesal horns. In addition, the phallus of *C. tripartita venezuelensis* has a pair of elongate, flattened lateral plates, rather than the ventral hooks present in *C. tripartita.* On the basis of these differences, *C. tripartita venezuelensis* is elevated to full species status.

Male.—Length 3.6–3.7 mm. Brown in alcohol. Antenna with 19 segments, scape elongate, basal flagellar segments broad. Abdominal sternum VII with elongate, slender process. Segment VIII narrowing posterolaterally to elongate acute process; in ventral view, tapering or truncate posteriorly with pair of mesal horns. Segment IX narrowing anteriorly, posteriorly with knoblike dorsolateral process. Segment X short and membranous; in dorsal view truncate posteriorly, fused with segment IX anteriorly. Inferior appendages divided into pair of lateral processes, ventralmost elongate and clublike, dorsalmost short and thin, mesal process narrow, elongate; in ventral view, ventralmost process narrow, curving inward apically, lateral process short, inner process elongate and tapering to acute apex. Phallus wide basally, narrow at midlength complex which bears sclerotized dorsal loop, parallel-sided apically with pair of lateral sclerites, short plate mesally.

Female.—Unknown.

Material examined.—VENEZUELA: Aragua State: Río El Limón fish hatchery, Maracay, 15–16.vii.1975, F. Weibezahn, ♂holotype, ♂paratype (NMNH); same, but 10.vii.1973, 1 ♂ (NMNH). COSTA RICA: Limón: Reserva Biológia Hitoy-Cerere, Río Cerere, 9.671°N, 83.028°W, el. 90 m, 23–24.iii.1987, Holzenthal, Hamilton, Heyn, 2 ♂ (UMSP).

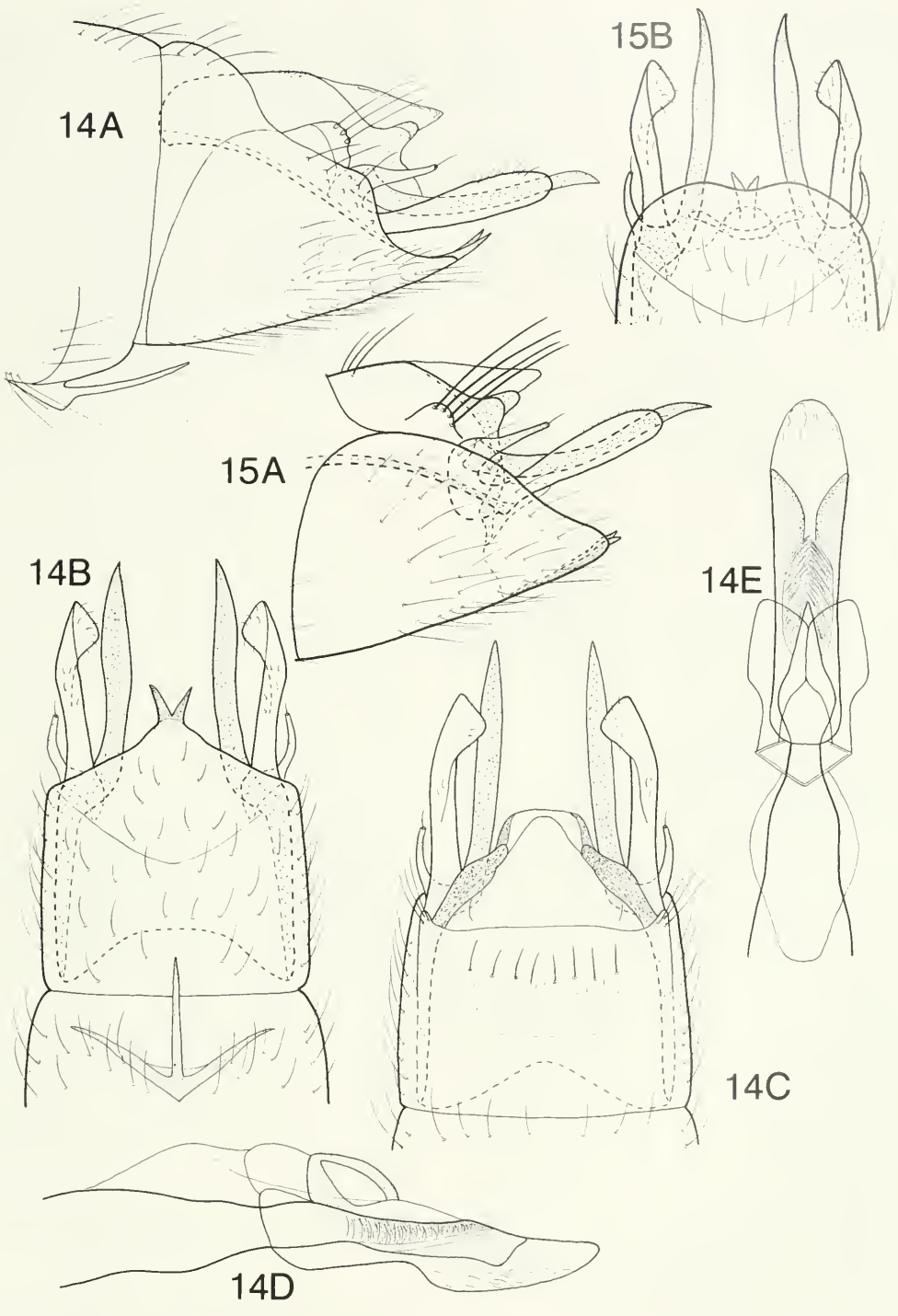
Comments.—There are some slight differences between the specimens of *C. venezuelensis* from Venezuela and the specimens from Costa Rica, mainly in the appearance of the sternum of segment VIII. In the Venezuela specimens the posterior margin of segment VIII is rounded in lateral view (Fig. 15A), and truncate in ventral view (Fig. 15B), while in the Costa Rica specimens segment VIII is much more tapered posteroventrally (Figs. 14A, B). These differences are interpreted as interspecific variation, as all specimens have in common the posterior mesal horns from the venter of segment VIII (Figs. 14B, 15B).

Costatrichia spinifera Flint

(Figs. 1B, 16)

Costatrichia spinifera Flint 1970: 13.

Costatrichia spinifera is readily recognized by the spinose apical portion of the



Figs. 14–15. *Costatrichia venezuelensis*, male genitalia. 14, specimen from Costa Rica. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal. 15, Paratype from Venezuela. A, Lateral. B, Ventral.

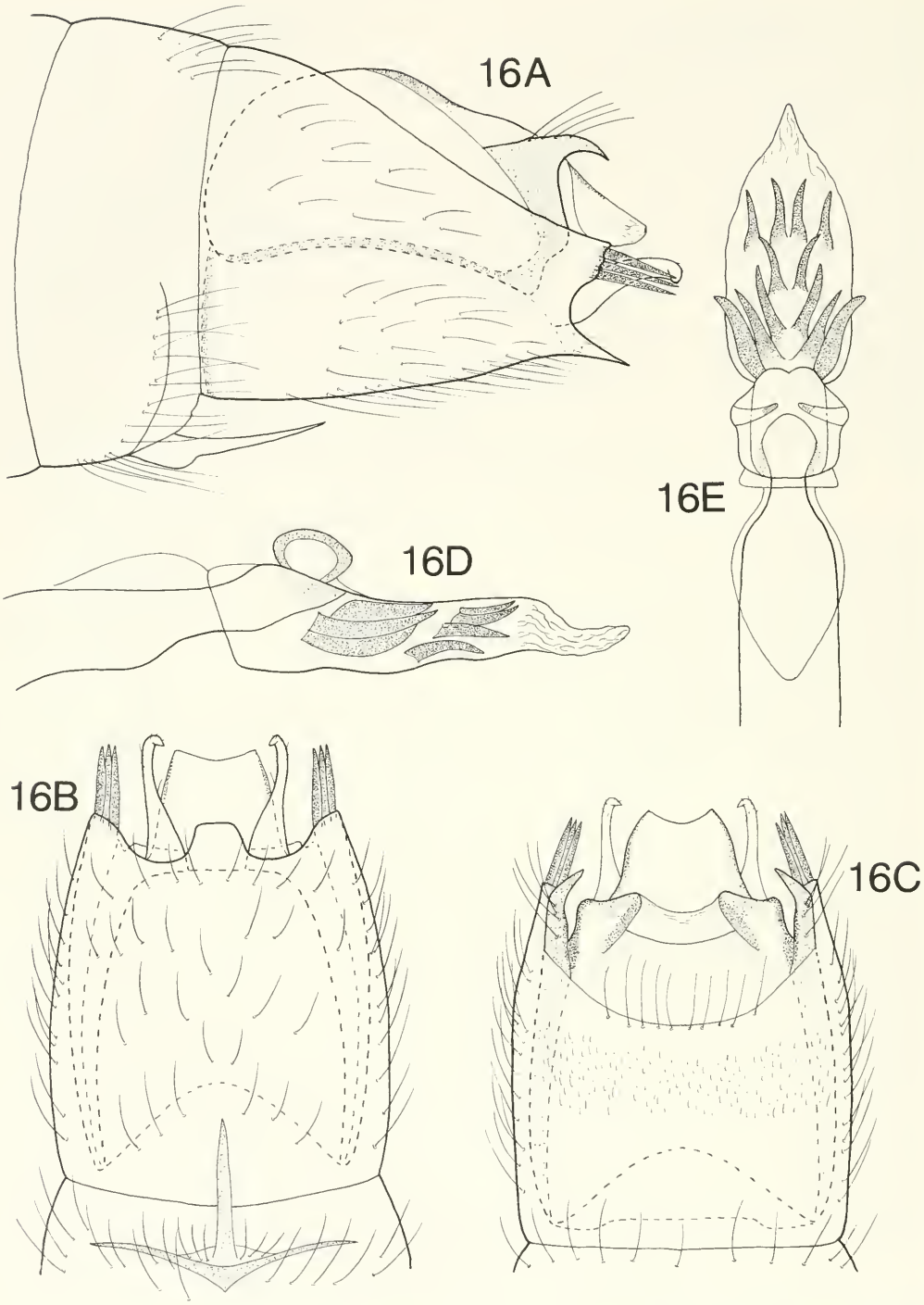


Fig. 16. *Costatrichia spinifera*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, ventral.

phallus. The species appears to be most similar to *C. simplex* from which it differs in the hooklike lateral process from segment IX and the posterolateral spines of segment VIII. The species was previously only recorded from Panama.

Male.—Length 3.7–3.9 mm. Antenna elongate with 19 segments, scape elongate, flagellar segments terete; 3 ocelli. Forewing mostly brown, basal portion and subapically with many greenish-white hairs; without costal bulla. Abdominal sternum VII with elongate, slender process. Segment VIII narrowing posterolaterally to acute ventral point, posterodorsally with truncate extension bearing three stout spines; in ventral view with truncate mesal process posteriorly, three elongate spines on posterolateral margins. Segment IX largely within segment VIII and dorsoventrally compressed, posterolaterally with acute dorsal process; truncate in dorsal view, posteriorly with sclerotized lateral process which curves inward apically. Segment X short and membranous, in dorsal view square in shape with slight mesal incision posteriorly, fused with segment IX anteriorly. Inferior appendages in lateral view short, narrow over length and curving slightly ventrad; in ventral view wide basally, tapering distally, bent inward at apex. Phallus wide basally, narrow at midlegth bearing sclerotized dorsal loop, apical portion bearing numerous stout spines posteriorly, anteriorly and mesally.

Female.—Unknown.

Material examined.—COSTA RICA: Puntarenas: Quebrada Potrero near Potrero Grande, 5.vii.1992, T. Shepard, 2 ♂ (UMSP).

Costatrichia zopilote, Holzenthal and Harris, new species

(Figs. 1C, 2B, 17–18)

Costatrichia zopilote is tentatively placed in the *simplex* group based on the simple antenna and absence of a costal bulla on the forewing. The new species is most similar to *C. spinifera* Flint on the basis of the spinose posterolateral extension of segment VIII, a feature also shared with *C. noite* Angrisano. *Costatrichia zopilote* is readily identified by the strongly upturned inferior appendages as seen in lateral view, a feature seen in some species of *Acostatrichia.* However, all species presently placed in *Acostatrichia* possess a costal bulla, a character diagnostic for the genus. Since this new species agrees with many of the characteristics seen in *Costatrichia,* differing only in a few features of the genitalia, we prefer not to establish a new genus and further the taxonomic confusion within the Leucotrichiini. As the Neotropical fauna becomes better known and with the completion of a study underway to reassess the generic limits of Leucotrichiini, it may be necessary to reassign *Costatrichia zopilite* in the future.

Male.—Length 3.2–3.7 mm. Brown in alcohol. Antenna short with 18 segments, scape and first flagellar segment elongate, remaining segments terete; 3 ocelli. Forewing without costal bulla. Abdominal sternum VII with short process. Segment VIII narrow, posterodorsally divided into three fingerlike lobes each bearing a thick, elongate spine, narrowed sharply posteroventrally; in ventral view, deeply incised mesally, lateral processes bearing elongate spines. Segment IX dorsoventrally compressed, posterolaterally with narrow process projecting dorsad; in dorsal view, deeply emarginate anteriorly, posteriorly with thin lateral processes. Segment X short in lateral view; in dorsal view, wide apically, narrowing near base and fused with segment IX, small sclerotized process from ventrolateral margin. Inferior appendages in lateral view tapering distally and bearing elongate setae, sharply curving dorsad; in ventral view fused basally, narrow processes laterally. Phallus tubular with sclerotized dorsal loop below midlength, anterior portion with pair of thin lateral sclerites with acute apices.

Female.—Length 3.5–3.9 mm. Coloration, head and antennal structure, and fore-

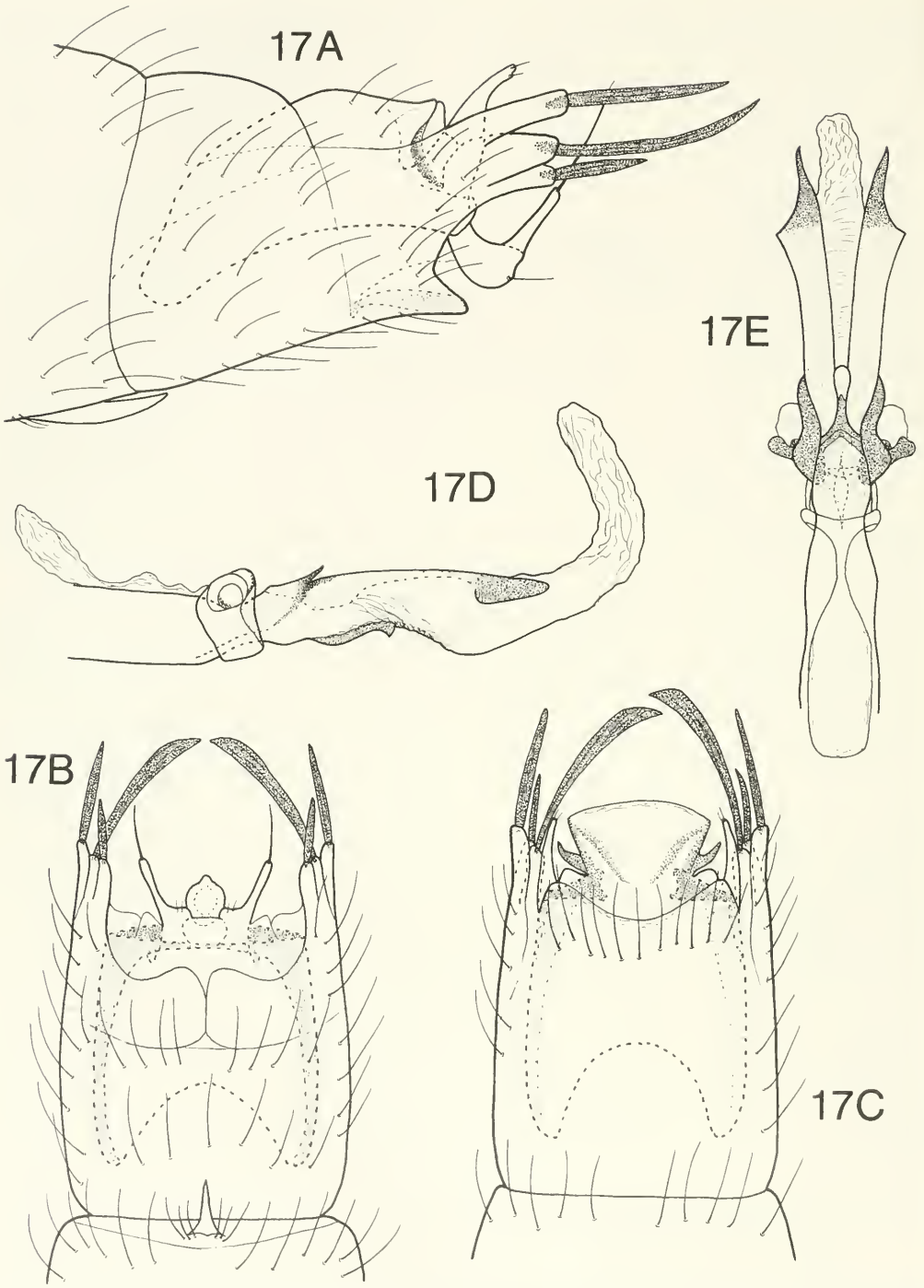


Fig. 17. *Costatrichia zopilote*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, ventral.

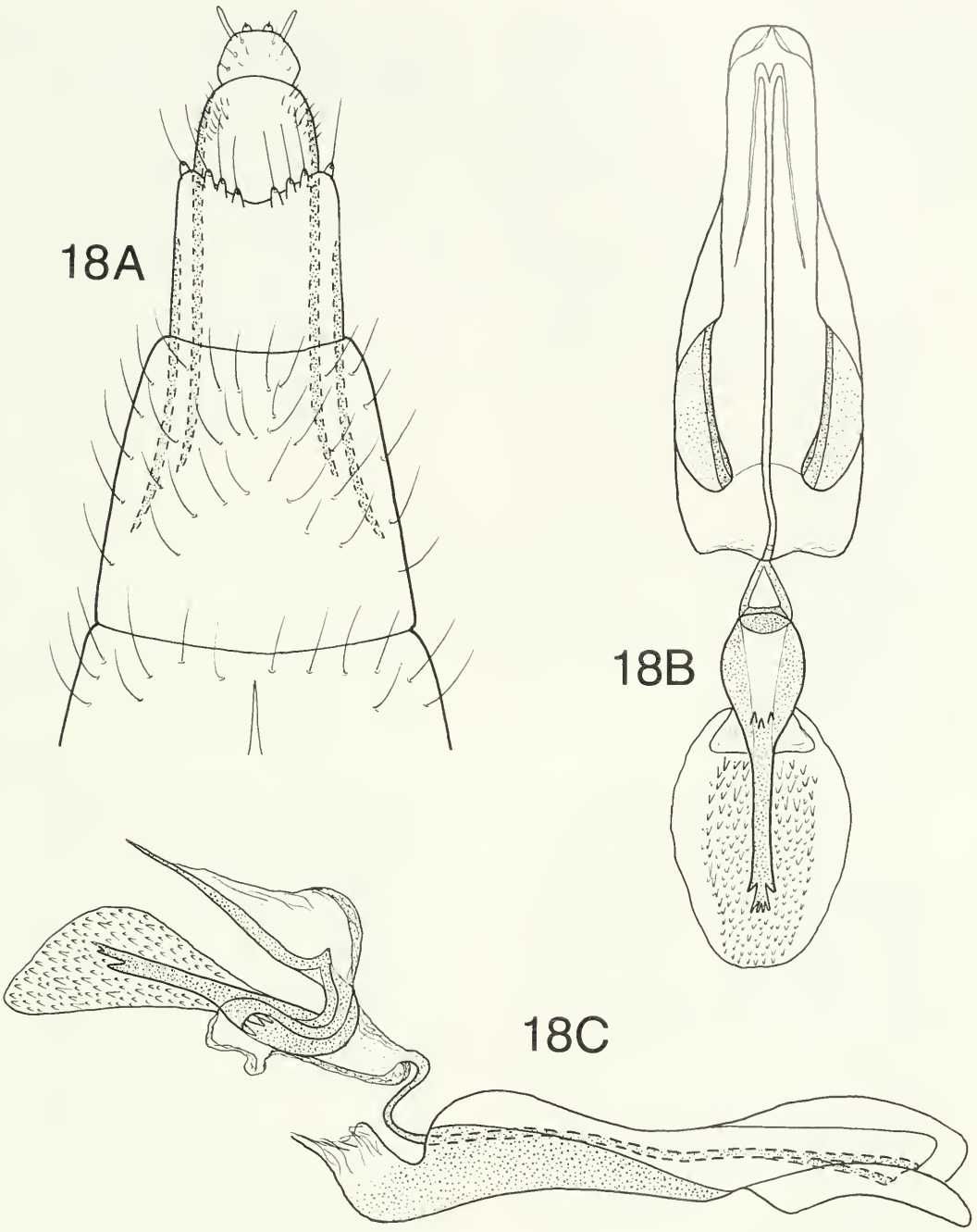


Fig. 18. *Costatrichia zopilote*, female genitalia. A, Terminal abdominal segments, ventral. B, Bursa copulatrix, ventral. C, Bursa copulatrix, lateral.

wings as in male; 3 ocelli. Abdominal segment VI with short sternal process. Segment VII annular. Segment VIII rectangular, posterior margin emarginate with ring of setae; laterally with pair of apodemes extending midway through segment VII. Segment IX short, rounded posteriorly; laterally with pair of apodemes extending to an-

terior segment VII. Segment X rounded posteriorly, bearing pair of lateral papillae. Bursa copulatrix in ventral view with oblong membranous lobe with pair of lateral sclerites connected by thin tube to lyrelike vaginal sclerite. Vaginal sclerite with several mesal teeth and anterior sac covered with short spicules; in lateral view, serrate teeth posteroventrally, bifid anteriorly attached to spicule covered sac, connected to membranous posterior lobes by thin tube.

Type material.—Holotype, ♂. COSTA RICA: Guanacaste: Parque Nacional Rincón de la Vieja, Quebrada Zopilote, 10.765°N, 85.309°W, el. 785 m, 3.iii.1986, R. Holzenthal (NMNH). Paratypes: COSTA RICA: Guanacaste: same data as holotype, 1 ♂, 1 ♀ (INBIO), 1 ♂, 1 ♀ (NMNH), 3 ♂, 8 ♀ (UMSP); Alajuela: Reserva Forestal San Ramón, Río San Lorencito and tributaries, 10.216°N, 84.607°W, el. 980 m, 30.iii –1.iv. 1987, Holzenthal, Hamilton, Heyn, 5 ♂ (UMSP); Quebrada Arena, Puesto San Ramón, iv.1994, F. Muñoz, 1 ♂ (UMSP).

Etymology.—Named for the type locality, Quebrada Zopilote.

Key to Males of the Genus *Costatrichia*

1. Abdominal segment VIII laterally bearing elongate spines or fingerlike processes with spines (Figs. 16, 17, 21) 2
– Abdominal segment VIII without spines from lateral margin (Figs. 4, 10) 4
2. Spines from segment VIII originating from truncated posterodorsal extension; phallus with numerous heavy spines (Fig. 16) . . . . . *C. spinifera*
– Spines from segment VIII elongate and featherlike, originating from fingerlike lobes; phallus without numerous heavy spines (Figs. 17, 21) 3
3. Inferior appendage fused over length; appearing straight in lateral view; spines from segment VIII posteroventral in position (Fig. 21) . . . . . *C. noite*
– Inferior appendages only fused to base, narrow and strongly upturned in lateral view; spines from segment VIII posterodorsal in position (Fig. 17) . . . . . *C. zopilote*
4. Inferior appendages divided in lateral view, either into 3 processes or bifid on posterior margin (Figs. 4, 8, 12) 5
– Inferior appendages entire, not divided in lateral view or absent (Figs. 6, 20) 10
5. Inferior appendages bifid or emarginate on posterior margin; elongate process from posterolateral margin of segment IX (Figs. 4, 5) 6
– Inferior appendages divided into 3 processes; no elongate process from posterolateral margin of segment IX (Figs. 12, 14) 7
6. Dorsal lobe of inferior appendage narrower than ventral lobe; lateral sclerites of phallus narrow and sinuate (Fig. 4) . . . . . *C. lodora*
– Dorsal lobe of inferior appendage wider than ventral lobe; lateral sclerites of phallus wide, tapering to acute apices (Fig. 5) . . . . . *C. flinti*
7. Posteroventral margin of segment VIII narrowing to elongate spine in lateral view, terminating in pair of mesal horns ventrally (Figs. 10, 14) 8
– Posteroventral margin of segment VIII not narrowing to elongate spine in lateral view, ventrally incised or emarginate posteriorly, but lacking pair of mesal horns (Figs. 8, 12) 9
8. Dorsalmost process of inferior appendage very short; venter of segment VIII with series of small internal spines (Fig. 10) . . . *C. carara*
– Dorsalmost process of inferior appendage elongate; venter of segment VIII without series of small spines (Figs. 14, 15) . . . . . *C. venezuelensis*
9. Venter of segment VIII deeply incised posteriorly, and lacking internal lateral spines; dorsalmost process of inferior appendage over ½ length of mesal process; phallus with posterior lateral processes acute (Fig. 8) . . . . . *C. tripartita*
– Venter of segment VIII emarginate with internal lateral spines; dorsalmost process of inferior appendages less than ½ length of mesal process; phallus with posterior lateral processes rounded (Fig. 12) . . . . . *C. cressae*
10. Elongate lateral process from segment IX; subgenital plate distinct; segment VIII laterally tapering to prominent posteroventral spine or process; phallus with spines distally (Figs. 19–20) 11
– No elongate process from segment IX; subgenital plate absent; segment VIII not tapering laterally to posteroventral process or spine; phallus with basal spines (Fig. 6) . . . . . *C. simplex*
11. Lateral process from segment IX strongly curved downward; segment VIII laterally tapering to seta-bearing, truncate posteroventral process; subgenital plate heavily sclerotized and hooked ventrally; phallus with tridentlike spines distally (Fig. 19) . . . . . *C. bipartita*

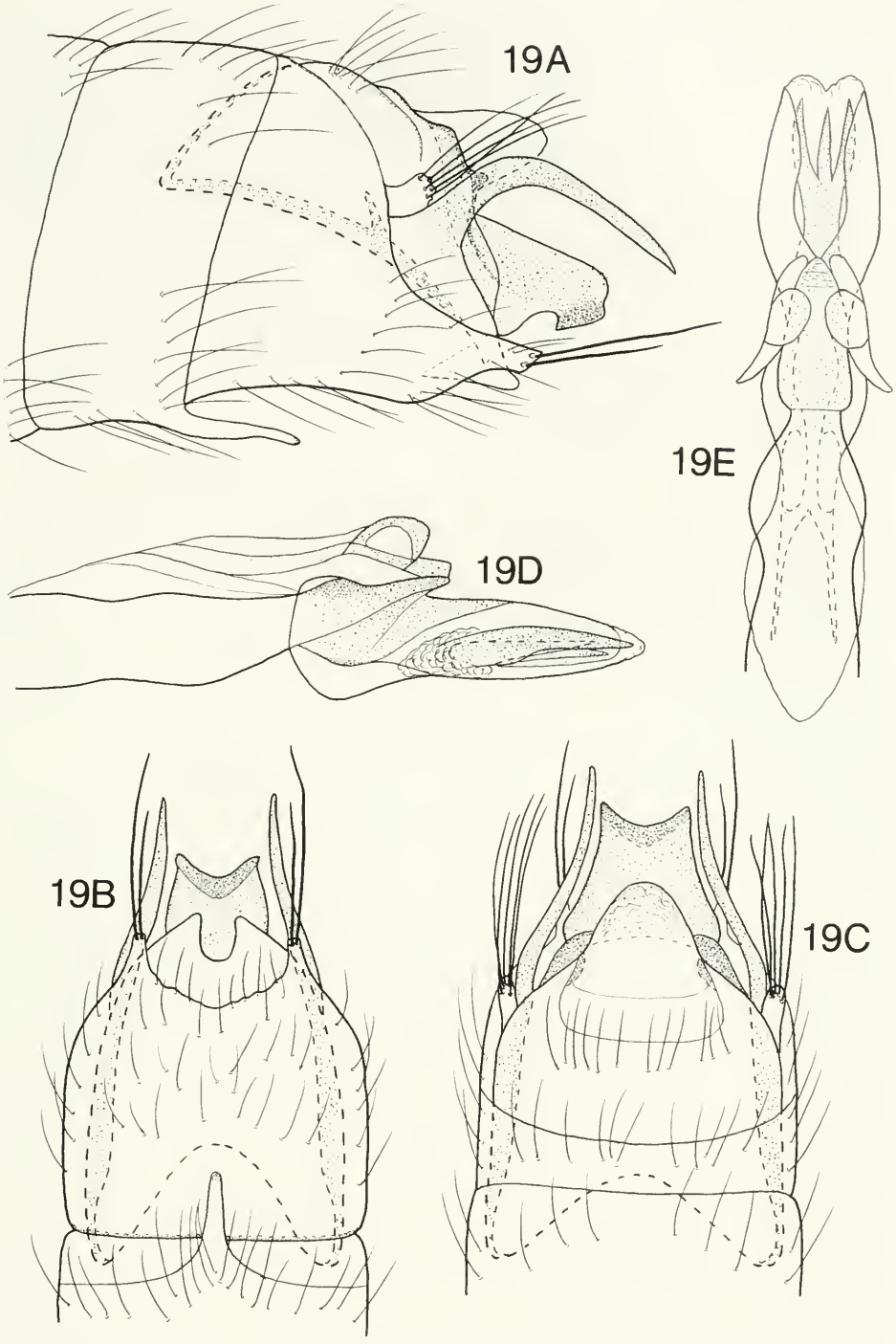


Fig. 19. *Costatrichia bipartita*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

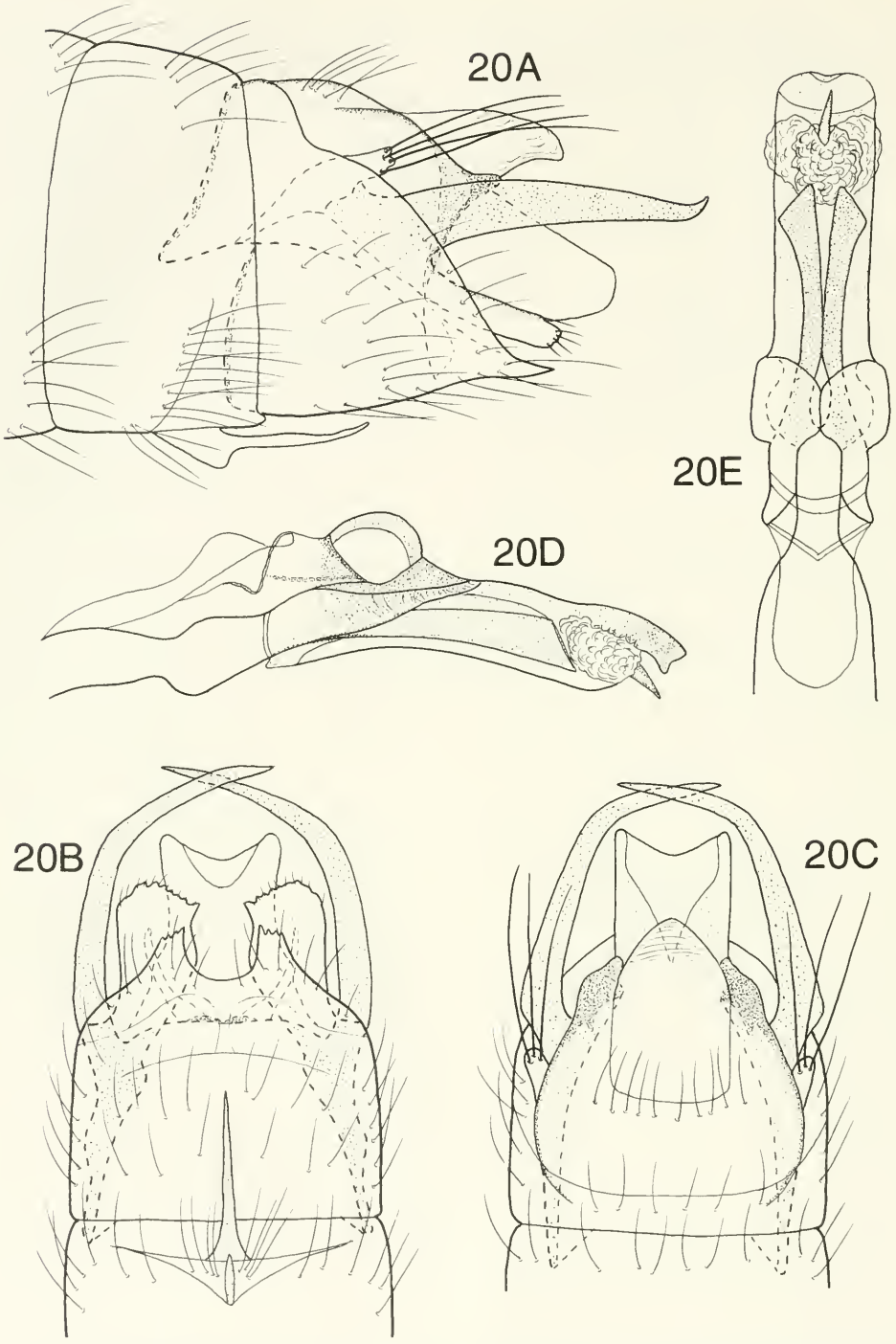


Fig. 20. *Costatrichia panamensis*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

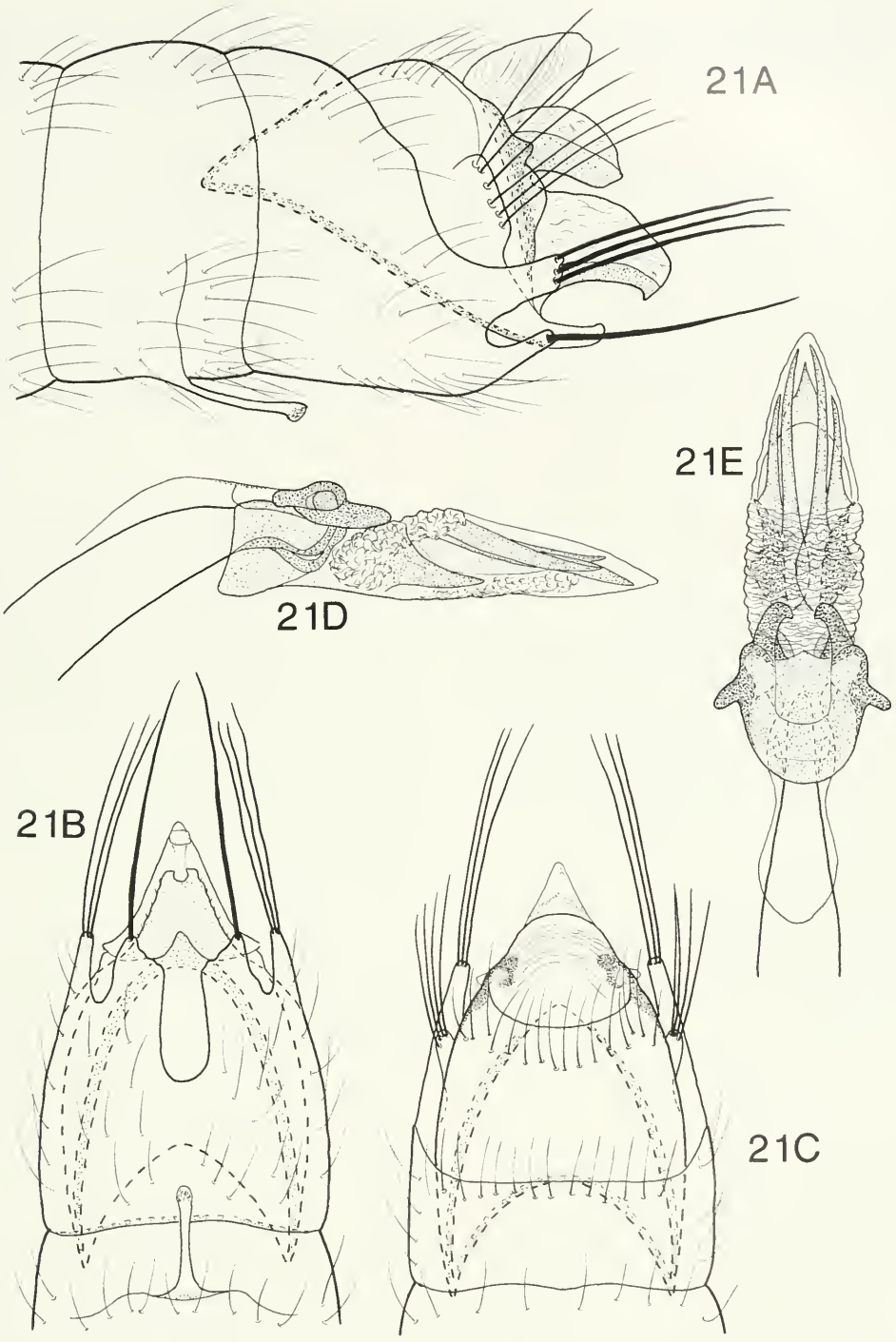


Fig. 21. *Costatrichia noite*, male genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

– Lateral process from segment IX straight; segment VIII tapering to acute posteroventral spine; subgenital plate lobate and unsclerotized; phallus with single distal spine (Fig. 20) . . . . . *C. panamensis*

Acknowledgments

We thank Dr. Oliver S. Flint, Jr., National Museum of Natural History, for the loan of much of the *Costatrichia* material examined during this study and for his review of the manuscript. Field work in Costa Rica by Holzenthal was supported by National Science Foundation grants BSR-8512368 and BSR-8917684. Subsequent systematics research by Holzenthal and Harris was supported by NSF grant DEB-9400632. Holzenthal's travel to Venezuela was supported by the University of Minnesota Insect Collection and the Universidad Central de Venezuela, Caracas, through Dr. Claudia Cressa. Thanks are also extended to personel of the Instituto Nacional de Biodiversidad, Costa Rica, Dr. Rodrigo Gámez, director, for their continued support of this research. Paper number 981170025, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

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A NEW SPECIES OF THE GENUS *BELESES* CAMERON (HYMENOPTERA: TENTHREDINIDAE) FROM MT. HAKUSAN, JAPAN

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Abstract.—***Beleses nigrifemoratus*, n. sp.**, is described and illustrated, and a key to the Japanese species of *Beleses* is provided.

Key Words: Symphyta, Tenthredinidae, *Beleses*, new species, Japan

As currently recognized, *Beleses* Cameron is a small genus of seven species that occurs from Japan through China and southeastern Asia to India. Two species are known in Japan, *Beleses satonis* (Takeuchi) (1929) and *B. zonalis* Togashi (1972). Recently, I found a specimen closely allied to *B. zonalis*, but it is separated from the latter by the black legs and the shapes of the claws and inner fore tibial spur. Therefore, I concluded that this specimen represents a new species, and I describe and illustrate it here.

Genus *Beleses* Cameron

Anisoneura Cameron 1876: 463. Type species: *Anisoneura stigmaticalis* Cameron, by Monotypy. Preoccupied by *Anisoneura* Lioy 1864.

Beleses Cameron 1877: 88. New name for *Anisoneura* Cameron.

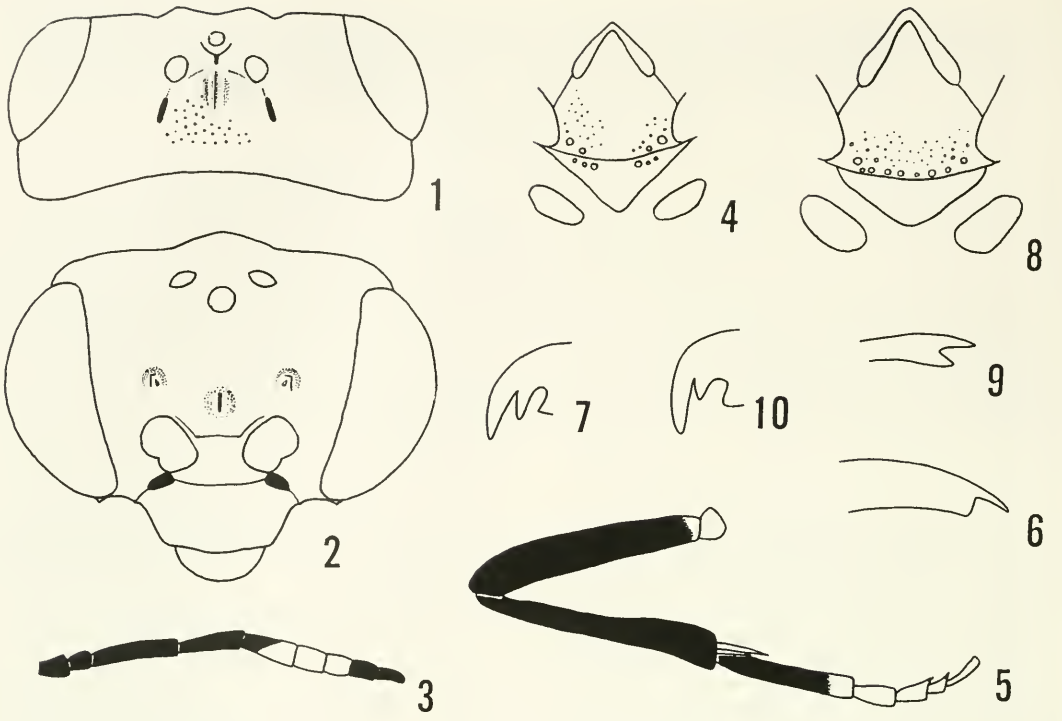
Generic characters.—Labrum small and semicircular in outline. Clypeus truncate. Malar space practically absent or linear. Antenna with pedicel distinctly longer than wide, 3rd segment longer than 4th. Metapostnotum narrow. Epicnemium absent. Forewing with 4 cubital cells, anal cell with a long oblique crossvein; hindwing with one middle cell and anal cell sessile (Fig. 11). Hind coxa lengthened, end of hind femur reaching to or beyond apex of abdomen. Claws with inner tooth and basal lobe (Figs. 7, 10).

Key to Japanese Species
(Females)

1. Head and body fulvous; legs fulvous . . . . . *satonis* Takeuchi
– Head and thorax black; labrum clypeus, pronotum, and tegula milky white; legs black or yellowish white 2
2. Hind femur and tibia entirely black; mesepisternum black; inner fore tibial spur as in Fig. 6; claws with rather large inner tooth (Fig. 7) . . . . . *nigrifemoratus*, n. sp.
– Hind femur and tibia yellowish white but apical half of femur and apical portion of hind tibia dark brown; mesepisternum with triangular white spot; inner fore tibial spur as in Fig. 9; claws with rather small inner tooth (Fig. 10) . . . . . *zonalis* Togashi

Beleses nigrifemoratus Togashi, new species
(Figs. 1–7, 11–14)

Female.—Length, 8 mm. Head and thorax black with following parts milky white: basal half of mandible, labrum, clypeus except for basal one-fifth, posterior corner of pronotum, tegula, and cenchrus. Abdomen black with following parts pale yellowish orange: 2nd tergum except for lateral side (Fig. 12), 3rd and 4th terga, basal half of 5th tergum (Fig. 12), and 2nd to 6th sterna. Antenna black but apical half of 5th segment and 6th and 7th segments milky



Figs. 1–10. 1–7, *Beleses nigrifemoratus*, holotype. 1, Head, dorsal view. 2, Head, front view. 3, Antenna, lateral view. 4, Mesoscutellum and posttergite, dorsal view. 5, Hind leg, except coxa, lateral view. 6, Inner fore tibial spur, lateral view. 7, Tarsal claw, lateral view. 8–10, *B. zonalis*, paratype. 8, Mesoscutellum and posttergite, dorsal view. 9, Innter fore tibial spur, lateral view. 10, Tarsal claw, lateral view.

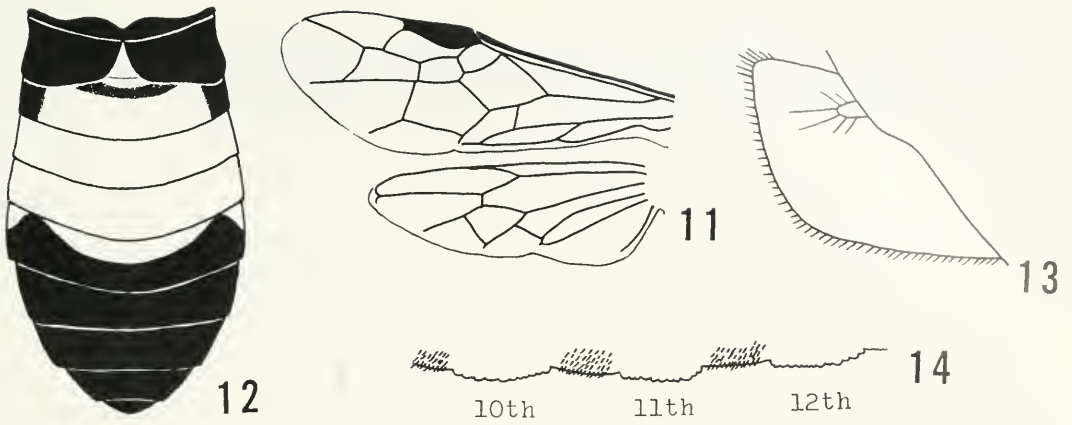
white. Wings hyaline, stigma and veins dark brown to black. Legs black with following parts milky white: all coxae, all trochanters, basal portion of hind femur, apical portion of hind basitarsus, and apical 4 hind tarsal segments.

Head transverse (Fig. 1); postocellar area convex, with a longitudinal process on anterior half (Fig. 1); circumocellar furrow distinct but anterior half indistinct; interocellar furrow distinct and deep; postocellar furrow rather indistinct; lateral furrows distinct and deep (Fig. 1); OOL : POL : OCL = 1.6:1.0:1.8; frontal area nearly flattened; median fovea slightly concave, with a distinct longitudinal furrow (Fig. 2); lateral fovea distinct, with ⅂-shaped furrow, and with a conical-like projection in middle (Fig. 2); antenno-ocular distance shorter than distance between antennal sockets (ratio about 1.0:1.3); antennal crest distinct; supraclypeal area slightly raised; clypeus slightly convex, anterior margin slightly swollen (Fig. 2); labrum slightly convex; malar space linear; postorbital groove and postgenal carina absent.

Antenna rather stout, shorter than costa of forewing (ratio about 1.0:1.3), flagellar segments 3–5 widened, wider than basal and apical flagellar segments (Fig. 3); relative lengths of segments about 1.2:1.0:3.6: 2.7:2.2:1.2:1.1:1.1:1.2; pedicel longer than wide (ratio between length and width about 1.0:0.7).

Thorax normal; mesoscutellum slightly raised. Wing venation as in Fig. 11. Legs with inner fore tibial spur as in Fig. 6; tarsal claws as in Fig. 7; hind basitarsus slightly longer than following 4 segments combined (ratio about 1.0:0.9) (Fig. 5); tarsal segments 1 and 2 lacking pulvulli.

Abdomen normal; sawsheath in lateral



Figs. 11–14. *Beleses nigrifemoratus,* holotype. 11, Wings. 12, Abdomen, dorsal view. 13, Sawsheath, lateral view. 14, 10th to 12th serrulae of lancet.

view as in Fig. 13; lancet with 17 serrulae; 10th to 12th serrulae as in Fig. 14.

Head and thorax covered with fine setigerous punctures but postocellar area, lower half of inner orbits, and clypeus distinctly, shallowly, and sparsely punctured (Fig. 1); upper side of mesosternum and mesepimeron practically impunctate, shining; posterior portion of mesoscutellum distinctly punctured (Fig. 4); anterior portion of posttergite distinctly punctured (Fig. 4). Abdominal terga covered with fine and sparse setigerous punctures, shining.

Male.—Unknown.

Distribution.—Japan (Honshu).

Holotype.—Female, 5.v.1998, Mt. Hakusan (alt. 1,300–1,500 m), Ishikawa Prefecture, Japan, I. Togashi leg. Deposited in the collection of the National Science Museum (Natural History), Tokyo.

Remarks.—This new species is separated from the other Japanes species of *Beleses* by the preceding key. It very closely resembles *Beleses zonalis,* but it is easily separated from the latter by the shape of the inner fore tibial spur and the claws (see Figs. 6–7, 9–10), by the presence of the depression at the outer side of the lateral furrows (in *B. zonalis,* the depression is absent), by the black perapteron (in *B. zonalis,* the perapteron is milky white), and by the black hind tibia (in *B. zonalis,* the hind tibia is yellowish white).

Beleses multipicta Rohwer from Taiwan, *B. nigriceps* Rohwer from southern India, and *B. zonalis* are the only other species of *Beleses* with a black head. *Beleses multipicta* has the apical four antennal segments white, inner orbits broadly white, and the posterior margin of the pronotum, tegula, perapteron, central spot on the mesepisternum, mesoscutellum, and metascutellum white. *Beleses nigriceps* has an orange thorax and black antennae.

The other species of *Beleses* are entirely orange to reddish brown, including the head. These are *B. atrofemoratus* Turner from Indochina, *B. satonis* from Japan, *B. fulvus* Cameron from China, and *B. stigmaticollis* (Cameron) from China.

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THE TRIBE MEROPACHYDINI WITH DESCRIPTIONS OF FIVE NEW GENERA, SYNONYMICAL NOTES, AND A KEY TO THE GENERA (HETEROPTERA: COREIDAE: MEROPACHYDINAE)

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Abstract.—Five new genera and six new species from Costa Rica, Brazil, Ecuador, Peru, and Bolivia are described in the tribe Meropachydini: ***Alcocerniella limonensis, Juaristiella pacificae, Larraldiella terminalis, Possaniella oblata, Soteloniella perparvula,*** and ***Soteloniella scutellata.*** *Menardus* Distant is proposed as a **new junior synonym** of *Peranthus* Stål, and *Menardus notatus* (Walker) is transferred to the genus *Peranthus,* resulting on the **new combination** *Peranthus notatus* (Walker). A key to the 11 known genera of Meropachydini is given.

Key Words: Insecta, Heteroptera, Coreidae, Meropachydinae, new genera, new species, Neotropical

Stål (1867) provided a key to the genera of Meropachydinae, and later Stål (1870) listed species included in each genus. Distant (1881–1892, 1900) made some changes in the generic placement primarily of species described by Walker (1871). Since that time, taxa of this subfamily have received little attention with a few exceptions (Kirkaldy 1904, Schmidt 1911, Kormilev 1951, 1954, Alayo Pastor 1967, Froeschner 1981, Baranowski and Slater 1986, Packauskas 1994).

The subfamily Meropachydinae Stål restricted to the Western Hemisphere, is a relatively small, but diverse group of Heteroptera characterized primarily by having the distal end of the hind tibiae ending beneath in a short projecting spine, hind femora curved and usually strongly incrassate, and hind coxae far separated. The subfamily includes 15 genera separated into three tribes: Merocorini (1), Meropachydini (7), and Spathophorini (7) (Kormilev 1954, Packauskas 1994).

The new genera belong to the tribe Meropachydini which are recognized by the elongate scutellum which extends beyond the distal end of the clavus, hind acetabulae projecting laterally and visible in dorsal view, and hind tibiae broadly curved distally.

In this revision five new genera and six new species collected in Costa Rica (1), Brazil (4), Ecuador (1), Peru (1) and Bolivia (1) are described, the genus *Menardus* Distant (1900) is proposed as a junior synonym of *Peranthus* Stål (1867), and *Menardus notatus* (Walker) is transferred to the genus *Peranthus,* with the binomen *Peranthus notatus* (Walker).

The following abbreviations are used for the institutions cited in this paper: AMNH (American Museum of Natural History, New York); BMNH (The Natural History Museum, London); BPBM (Bernice P. Bishop Museum, Honolulu); CAS (California Academy of Sciences, San Francisco); CMN (Carnegie Museum of Natural His-

tory, Pittsburgh); INBIO (Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica); LACM (Los Angeles County Natural History Museum, Los Angeles); MNR (Museum Nacional, Rio de Janeiro, Brasil); UB (University of California, Berkeley); UNAM (Instituto de Biología, Universidad Nacional Autónoma de México); USU (Utah State University, Logan); ZMB (Museum der Humboldt, Universität zu Berlin, Germany).

Features in Common of the Genera Described

Head: Wider than long, pentagonal, non declivent, dorsally flat; tylus unarmed, apically globose, elevated, extending anteriorly to and laterally higher than juga and antenniferous tubercles; juga unarmed, shorter than tylus; space between antenniferous tubercles filled by tylus; antenniferous tubercles unarmed, never contiguous; space between antenniferous tubercles almost wider than one tubercle; side of head in front of eye unarmed; antennae shorter than body; antennal segment I robust, barely flattened, thickest, slightly curved outward, longer than head; segments II and III flattened, sulcate, slender; segment IV fusiform, weakly incrassate; antennal segment IV the longest, III the shortest, and I longer than II; ocelli close to eyes; preocellar pit obliquely deep; eyes globose, slightly protuberant, based on an hypothetical line upper margin located almost at same level of vertex and frontal area; postocular tubercle absent; mandibular plate absent; head ventrally and behind buccula without or with conical tubercle; buccula rectangular or almost quadrate, raised, short, entire, projected or not beyond antenniferous tubercles, meeting posteriorly and closed; rostrum short, barely reaching anterior or middle third of mesosternum.

Thorax: Pronotum: Wider than long, trapeziform, slightly declivent, wider than base of scutellum; collar wide; frontal angles obtuse, not projected; humeral angles obtuse or barely projected; calli entire, not elevated, separated at midline by a short and wide longitudinal furrow; anterior margin entire, slightly curved; anterolateral margins obliquely straight, smooth or tuberculate, and emarginate or not; posterolateral margins sinuate and smooth; posterior border convex or barely straight, margin without or with an irregular transverse ridge; triangular process absent or well developed. Prosternum markedly sunken, with posterior third in front of area between fore legs produced into narrowed acute tubercle; mesosternum raised or not, with anterior margin in front of area between fore legs produced into narrowed subacute tubercle, posterior margin variable throughout genera; lateral margins of mesopleuron raised on a short or medium-size elongate tubercle, overlapping or not propleuron; metasternum variable throughout genera; posterior margin of metathorax straight, with lateral angles projected into wide conical tubercles, touching the hind coxae; metathorax laterally expanded, in dorsal view with metapleura and acetabulae weakly or prominently visible; metathoracic peritreme located near lower margin of metapleuron, with upper third closed; canal short, semicircular, with raised sides; evaporating area poorly developed; anterior lobe variable throughout genera, posterior lobe short, obtuse, slightly exposed.

Legs: Hind coxa strongly separated, armed or unarmed, visible beyond costal margins and sides of body in dorsal view; hind trochanter conspicuously tuberculate and exposed, or weakly convex; fore and middle femora relatively slender, unarmed or armed with one to three subdistal tubercles; hind femur markedly incrassate, with dorsal surface smooth or tuberculate and ventral surface strongly armed with spines and tubercles; fore and middle tibiae unarmed, sulcate, and slightly expanded at posterior third; hind tibia curved, compressed, shorter than femur, with outer margin not expanded and remarkably sulcate, inner margin usually markedly expanded, and apically armed with a broad long spine; fore and middle tarsi with tarsal segment I

equal or slightly shorter than segments II and III combined; hind tarsus with segment I longer or shorter than segments II and III combined.

Scutellum: Longer than wide, and always longer than clavus; general shape variable throughout genera; disc with or without Y-shaped elevation.

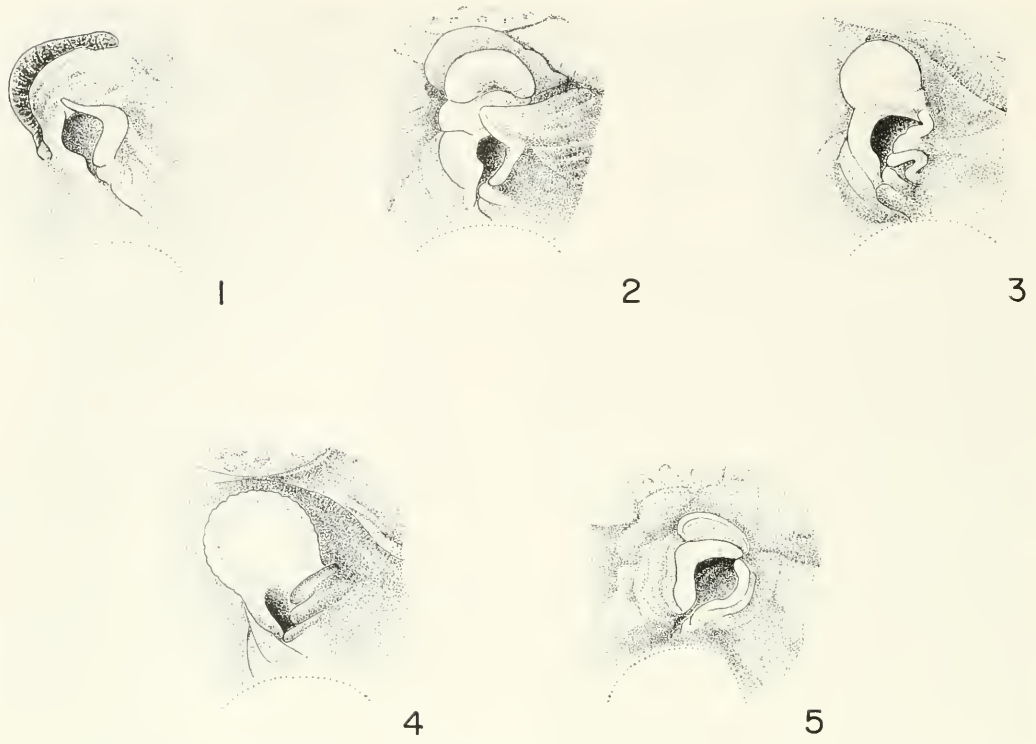
Hemelytron: Macropterous, reaching apex of or slightly beyond last abdominal segment; claval suture present but covered by apex of scutellum; clavus partially covered by scutellum; costal margin shallowly concave; apical margin obliquely straight or slightly concave, with apical angle narrowly, very long, extending beyond middle third of hemelytral membrane.

Abdomen: Gradually narrowing beyond middle, and slightly expanded posteriorly; abdominal segment VII of male usually laterally exposed; connexival segments scarcely elevated, clearly sulcate; posterior angle of each segment entire, not expanded into spine; abdominal sternum without medial furrow; abdominal spiracle elliptical; abdominal spiracle III closer to anterior border, spiracles IV to VII closer to middle third; abdominal sternite II visible, slender, with or without conical tubercle located close to posterior border of metathorax; abdominal sternite III weakly or clearly expanded, and in dorsal view with spiracle visible.

Female genitalia: Abdominal sternite VII with plica and fissura; plica triangular; fissura with inner margin overlapping; gonocoxae I subtriangular, in caudal view closed, in lateral view almost straight, with upper border rounded; paratergite VIII triangular, with spiracle visible; paratergite IX squarish, longer than paratergite VIII.

Key to Genera of Meropachydini

1. Posterior border of pronotum with a triangular projection above each basal angle of scutellum 6
– Posterior border of pronotum without triangular projections 2
2. Head ventrally behind buccula with a strong conical tubercle (= *Menardus* Distant) . . . . . *Peranthus* Stål
– Head ventrally behind buccula smooth, without a tubercle at most with an irregular callosity 3
3. Scutellar disc without a distinct Y-shaped elevation; posterior margin of mesosternum at each side with one short lobe touching anterior lobes of metasternum (Figs. 11–12); posterior margin of metasternum flat; dorsal surfaces of hind femora smooth 4
– Scutellar disc with a clearly Y-shaped elevation; posterior margin of mesosternum at each side with one large lobe freely projecting backwards and bending up, not touching anterior lobe of metasternum (Figs. 6–10, 13); posterior margin of metasternum at middle third with a deep depression of capsule-like appearance; dorsal surface of hind femura weak to strongly tuberculate from base to apex 5
4. Scutellum remarkably slender abruptly narrowed on distal half, apex bifid (Fig. 21); antennal segment I slender, less than 2.05 mm; metapleura not laterally expanded; hind femur scarcely incrassate; inner face of hind tibia weakly expanded; abdominal sternite III of male with small lateral prominences . . . . . *Larraldiella*, new genus
– Scutellum not remarkably slender, narrowing very gradually, apex rounded; antennal segment I robust, longer than 2.10 mm; metapleura laterally expanded; hind femur conspicuously incrassate; inner face of hind tibia expanded; abdominal sternite III of male smooth, without lateral prominences . . . . . *Gracchus* Stål
5. Dorsal surface of hind femur strongly tuberculate from proximal to distal end; hind trochanter convex, not tuberculate; scutellum 1.7 to 2.2 times longer than wide, and apically rounded; anterior margins of thoracic mesopleura each with a black elongate spot . . . . . *Marichisme* Kirkaldy
– Dorsal surface of hind femur weakly tuberculate from proximal end to middle third (Fig. 22); hind trochanter tuberculate; scutellum 3.3 to 3.8 times longer than wide, and apically acute; anterior margins of thoracic mesopleura without black spot . . *Soteoniella*, new genus
6. Head ventrally and behind buccula with a strong conical tubercle 7
– Head ventrally and behind buccula smooth, without a tubercle 9
7. Hind femur conspicuously clavate, slender towards base, and abruptly thickened beyond middle (Fig. 23) . . . . . *Possaniella*, new genus



Figs. 1–5. Metathoracic peritreme. 1, *Flavius lineaticornis*. 2, *Soteloniella perparvula*. 3, *Juaristiella pacificae*. 4, *Alcocerniella limonensis*. 5, *Larraldiella terminalis*.

– Hind femur never clavate, uniformly incrassate (Figs. 19–20) 8

8. Middle third of posterior margin of metasternum flat, without lateral lobes (Fig. 10); anterior lobe of metathoracic peritreme with a black lunular spot (Fig. 1); body surface densely pubescent; scutellum clearly contracted near base; dorsal surfaces of hind femur strongly tuberculate . . . . . *Flavius* Stål

– Middle third of posterior margin of metasternum with two lateral lobes (Figs. 6–8); anterior lobe of metathoracic peritreme tooth-shaped without a black lunular spot (Figs. 3–4); body surface not densely pubescent; scutellum not contracted near base; dorsal surfaces of hind femur smooth . . . . . *Alcocerniella*, new genus

9. Posterior margin of mesosternum trilobed, with mesial lobe expanded and broad, and lateral lobes short (Fig. 9); scutellum strongly contracted near the base; scutellar disc with a broad Y-shaped elevation . . . . . *Meropachys* Burmeister

– Posterior margin of mesosternum bilobed (Figs. 6–7); scutellum not or weakly contracted near base; scutellar disc without a distinct Y-shaped elevation 10

10. Posterior margin of metasternum bilobed (Fig. 6) . . . . . *Hirilcus* Stål

– Posterior margin of metasternum projected in a medial quadrangular plate directed straight downward (Fig. 7) . . . . *Juaristiella*, new genus

Alcocerniella Brailovsky, new genus

Diagnosis.—*Alcocerniella* and *Flavius* Stål are the only known genera in the tribe Meropachydini that have the head ventrally with a conical tubercle behind the bucculae, triangular process on posterior margin of pronotum well developed, mesosternum almost raised, and the hind coxa with outer apical angle strongly tuberculate.

Alcocerniella differs from *Flavius* by the following characters: Anterior lobe of metathoracic peritreme globose, without a black lunular spot (Fig. 4), scutellum not contracted near base, hind femur in dorsal view

smooth, body surface not densely pubescent, mesosternum slightly raised, and middle third of posterior margin of metasternum with two lateral lobes (Fig. 8). In *Flavius* the anterior lobe of the metathoracic peritreme has a black lunular spot (Fig. 1), scutellum clearly contracted near base, hind femur in dorsal view strongly tuberculate, body surface heavily covered with whitish pubescence, mesosternum conspicuously raised, middle third of posterior margin of metasternum flat, without lateral lobes (Fig. 10).

A unique character in the male of *Alcocerniella* is the conical tubercle on abdominal sternite III, absent in *Flavius*.

Generic description.—*Head:* Distance between ocelli 2.4 to 2.6 times diameter of one ocellus; distance between ocelli and eye 0.9 to 1.1 times diameter of one ocellus; head ventrally and behind buccula strongly tuberculate; rostrum short, barely reaching anterior third of mesosternum; rostral segment III shortest, IV longest, I longer than II.

Thorax: Pronotum: Humeral angles obtuse, not exposed; anterolateral borders obliquely straight, almost smooth, not emarginated; posterior border barely convex; triangular process broad, apically rounded. Mesosternum weakly raised, anterior margin in front of area between fore legs produced into a narrowed subacute tubercle, posterior margin between middle legs prominent, bilobed, each lobe well separated from mesial line, overlapping the lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin remarkably raised on two large lobes, separated along midline by a wide furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum almost straight, each lateral angle projected as a broad rectangular plate, laying against metacoxae, and at middle third with two lateral lobes delimiting a barely hemispherical capsule-like depression (Fig. 8); lateral margin of mesopleura raised as an elongate tubercle overlapping the posterior margin of propleuron; metathorax laterally expanded, in dorsal view metapleura and acetabulae very broadly visible. Anterior lobe of metathoracic peritreme globose (Fig. 4).

Legs: Hind coxae well separated, distance between them nearly 3.4 to 3.8 times the diameter of one coxa, outer apical angle strongly tuberculate; hind trochanter convex; fore femur relatively slender, unarmed; middle femur relatively slender, ventrally with 1 to 3 subdistal tubercles; hind femur markedly incrassate, attaining apex or posterior margin of last abdominal sternite with dorsal surface smooth, ventrally armed with spines and tubercles in two irregular rows, without a strong tooth close to base; inner margin of hind tibia well expanded.

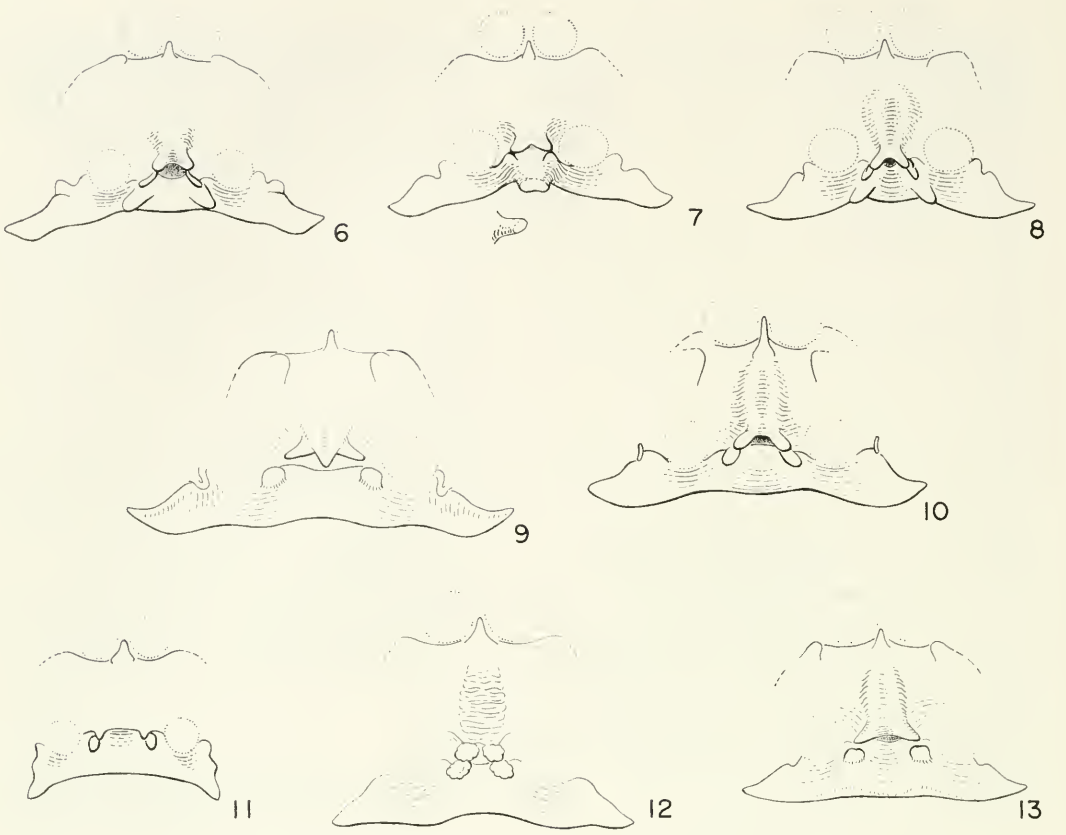
Scutellum: 1.8 to 2.1 times longer than wide, longer than clavus, not coarctate near base; disc with Y-shaped elevation; apex subacute; lateral margins clearly emarginate.

Abdomen: Abdominal sternite II visible, slender, without conical tubercle; abdominal sternite III clearly expanded, in dorsal view with spiracle visible; male abdominal sternite III laterally conspicuously produced into two large conical lobes freely directed downwards; female abdominal sternite III flat, without conical lobes.

Male genitalia: Genital capsule simple, semiglobose; posteroventral edge entire, straight, with small medial plate, and laterally with the angles rounded. Paramere: Simple and straight; anterior lobe convex, continuous with body, apex curved, narrowly blunt (Fig. 15).

Female genitalia: Spermatheca: Bulb somewhat elongated; spermathecal duct moderately coiled proximally, with only two distal coils; flank distinct; chamber more or less globose (Fig. 14).

Integument: Body surface with mixed short and large decumbent to suberect hairs; head, calli, clavus, corium, prosternum, mesosternum, metasternum, and abdominal sterna impunctate; pronotum strongly punctate, abruptly striate; scutellum punctate,



Figs. 6–13. Thorax in ventral view showing mesosternum and metasternum. 6, *Hirilcus gracilis*. 7, *Juaristiella pacificae*. 8, *Alcocerniella limonensis*. 9, *Meropachys nigricans*. 10, *Flavius lineaticornis*. 11, *Larraldiella terminalis*. 12, *Gracchus integer*. 13, *Soteloniella perparvula*.

except lateral margins and Y-shaped elevation (arms of Y-shaped finely striate); propleura, posterior margin of metapleura, and acetabulae punctate; metapleura weakly tuberculate; antennal segments and legs densely covered with short decumbent to suberect setae.

Etymology.—Named for Jorge Alcocer Varela, distinguished Mexican immunologist.

Type species.—*Alcocerniella limonensis* Brailovsky, new species.

Alcocerniella limonensis Brailovsky, new species

(Figs. 4, 8, 14–15, 19)

Description.—*Measurements:* Male: Head length 1.75; width across eyes 2.30; interocular space 1.20; interocellar space 0.45; distance ocellus to eye 0.20; diameter of ocellus 0.17; preocular distance 1.10; length antennal segments: I, 3.55; II, 2.95; III, 2.60; IV, 4.20; length rostral segments: I, 0.77; II, 0.58; III, 0.55; IV, 0.80. Pronotum: Total length 4.45; width across frontal angles 2.25; width across humeral angles 5.40. Scutellar length 5.50; maximum width of anterior lobe 2.25; maximum width of posterior lobe 1.40. Hind leg: femur length 8.74; tibia length 5.82. Total body length 18.20.

Female: Head length 1.60; width across eyes 2.05; interocular space 1.05; interocellar space 0.45; distance ocellus to eye 0.17; diameter of ocellus 0.15; preocular distance 1.03; length antennal segments: I, 2.85; II,

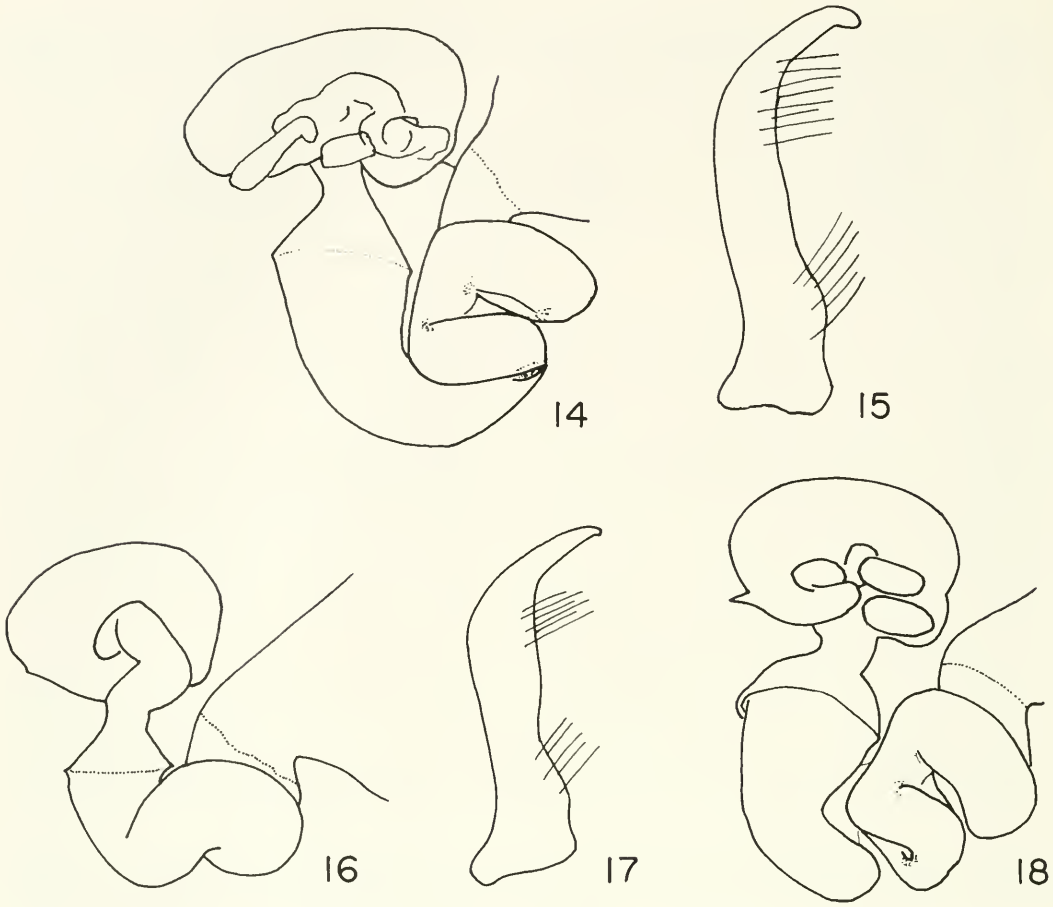
2.30; III, 2.15; IV, 3.80; length rostral segments: I, 0.65; II, 0.62; III, 0.52; IV, 0.74. Pronotum: Total length 3.90; width across frontal angles 2.25; width across humeral angles 4.55. Scutellar length 4.15; maximum width of anterior lobe 1.90; maximum width of posterior lobe 0.95. Hind leg: femur length 6.91; tibia length 5.16. Total body length 15.72.

Dorsal coloration: Male: Head bright chestnut yellow with olive green reflections; antennal segment I with dorsal face dull chestnut orange and ventral face reddish brown; segments II and III reddish brown, IV with basal third reddish brown, middle and distal third dark reddish orange; pronotum chestnut yellow with three broad longitudinal stripes, posterior margin, and humeral angles pale to dark olive green; scutellum bright orange yellow with bright red longitudinal medial stripe; clavus and corium dark olive green to dark brown, with veins yellow and with or without olive green reflections; hemelytral membrane dark ambarine with veins and basal angle black; connexival segments I to VI yellow, and VII black; abdominal segments black, with abdominal scars IV–V and V–VI yellow. *Ventral coloration:* Head pale bright chestnut orange with olive green reflections; rostral segments dark bright chestnut orange with olive green reflections (apex of IV black); prothorax orange yellow with reddish orange spot near fore acetabulae, posterior margin of propleura olive green with punctures reddish brown; mesosternon mostly black; mesopleuron bright orange yellow with reddish orange spot near to middle acetabulae, and close to middle third of the same mesopleuron; metathorax bright orange with anterior and posterior tubercles darker to black; upper face of hind acetabulae bright orange with olive green reflections and irregular red spot near to dorsal edge; metathoracic peritreme black with anterior lobe with pale ochre reflections; fore and middle legs, with coxae, and trochanters bright chestnut orange, femora and tibiae yellow with olive green reflections and tarsi reddish brown; hind leg with coxa bright orange, trochanter bright reddish brown, femur bright orange with spines and tubercles reddish brown, tibia and tarsus bright black to reddish brown; abdominal sterna bright chestnut orange with tubercles of abdominal sternite III and posterior margin of VII reddish brown; pleural abdominal sterna III to VI bright orange yellow, and VII black with olive green reflections; genital capsule bright chestnut orange.

Female: Similar to male. Connexival segments VIII and IX dark chestnut orange; abdominal segments VIII and IX black; genital plates bright chestnut orange, outer border of paratergite VIII and IX black; plica black; hind tibia bright black with pale yellow fascia close to the apical third; abdominal sternite III without lateral tubercles.

Variations in coloration: 1, Pronotum chestnut orange with olive green reflections, and three irregular longitudinal stripes black to dark olive green. 2, Clavus and corium with veins pale olive green. 3, Corium dark olive green to dirty yellow with olive green reflections. 4, Anterior lobe of metathoracic peritreme pale yellow. 5, Hind tibia bright black, basal join and outer surface chestnut orange. 6, Posterior margin of metathorax creamy yellow to yellow, with olive green reflections. 7, Mesosternum bright chestnut orange. 8, Area around each abdominal spiracle reddish orange. 9, Tubercles of abdominal sternite III bright orange.

Type material.—Holotype: ♂, Costa Rica, Prov. Limon, Estac. Hitoy Cerere, R. Cerere, Res. Biol. Hitoy-Cerere (1000 m), July 1992, G. Carvallo (INBIO). Paratypes: COSTA RICA: 2 ♂ 1 ♀, Prov. Guanacaste, Estac. Pitilla, 9 km. S. Sta Cecilia (700 m), May and August 1988, G. N. P. Biodiversity Survey, 85°25′40″W–10°59′26″N and November 1988, C. Chaves and M. Espinoza (INBIO, UNAM); 4 ♂, Prov. Heredia, Estac. Magsasay, P. N. Braulio Carrillo (200 m), March 1991, A. Fernandez, May 1991, M. A. Zumbado (INBIO, UNAM); 1 ♀,



Figs. 14–18. 14–15, *Alcocerniella limonensis*. 14, Spermatheca. 15, Paramere. 16–17, *Juaristiella pacificae*. 16, Spermatheca. 17, Paramere. 18, Spermatheca of *Hirilcus gracilis*.

Prov. Puntarenas, Estac. Biol. Las Alturas, Coto Brus (1500 m), January 1992, M. Ramirez, G. Mora and F. Quesada (INBIO); 1 ♀, Golfito, 26 July 1981, B. K. Dozier (USU); 1 ♂, Prov. Cartago, 3 km. SE, Turrialba, CATIE (600 m), 13–16 May 1985, J. Doyen (UB); 1 ♀, Prov. Limon, Hacienda Tapezco, 29 air Km, W. Tortuguero, 10°30′N–83°47′W (40 m), 13 March 1978, J. P. Donahue, D. Penny, D. Moeller, and C. Lewis (LACM); 1 ♂, Prov. Limon, Siquirres (100–200 m), 16 August 1970, J. and M. Sedlacek (BPBM).

Etymology.—The species is named for the Province of Limon in Costa Rica.

Distribution.—Known only from Costa Rica.

Juaristiella Brailovsky, new genus

Diagnosis.—*Alcocerniella, Flavius, Hirilcus, Meropachys, Possaniella,* and *Juaristiella* are the only known genera in the tribe Meropachidini with a triangular process on posterior border of pronotum.

In *Alcocerniella, Flavius* and *Possaniella,* the head in ventral view has a tubercle behind buccula, in *Hirilcus* the tubercle is absent or barely developed, and in *Meropachys* and *Juaristiella* always absent. In *Meropachys* the posterior margin of mesosternum between middle legs is trilobed, with medial lobe expanded and broad, lateral lobes shorter, the posterior margin of metasternum simple and straight (Fig. 9). In

Hirilcus and *Juaristiella* the posterior margin of mesosternum is bilobed (Figs. 6–7).

Juaristiella is clearly segregated from *Hirilcus* because the posterior margin of the metasternum is projected into a medial quadrangular plate directed straight downward (Fig. 7), and the spermathecal bulb is elongated with the proximal third barely coiled (Fig. 16). In *Hirilcus* the posterior margin of the metasternum is projected into two lateral and broad conical tubercles (Fig. 6), and the spermathecal bulb is almost flattened, with the proximal third conspicuously coiled (Fig. 18).

Generic description.—*Head:* Distance between ocelli 4.0 to 4.2 times the diameter of one ocellus; distance between ocellus and eye 0.8 times the diameter of one ocellus; head ventrally and behind buccula without tubercle; rostrum short, barely reaching anterior third of mesosternum; rostral segment III shortest, IV longest, I longer than II.

Thorax: Pronotum: Humeral angles obtuse, barely exposed; anterolateral borders obliquely straight, tuberculate, weakly emarginate; posterior border convex; triangular processes broad, apically rounded; pronotal disc and calli with tubercles or irregular elevations. Mesosternum not raised, anterior margin in front of area between fore legs produced into narrowed subacute tubercle, and posterior margin between middle legs bilobed, with each lobe almost touching at mesial line and projecting towards metasternum, laying between tubercles of anterior margin of metasternum; metasternum slender, rectangular, with anterior border distinctly raised as two broad lobes, separated along midline by short furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum projected into a mesial quadrangular plate directed straight downward (Fig. 7); lateral margin of mesopleura raised on an elongate callosity; metathorax laterally expanded, in dorsal view with metapleura and acetabulae remarkably visible. Anterior lobe of metathoracic peritreme strongly exposed, semiglobose, curving upward (Fig. 3).

Legs: Hind coxa strongly separated, with outer apical angle scarcely tuberculate; distance between them 4.0 to 5.0 times diameter of one coxa; hind trochanter convex; fore and middle femora slender, unarmed, without tubercles; hind femur markedly incrassate, not attaining apex of abdomen, reaching middle third of abdominal sternite VI; dorsal surface with few scattered callosities, similar to tubercles, ventrally armed with five subapical spines and four tubercles in one irregular row; inner margin of hind tibia markedly expanded.

Scutellum: 2.1 (♂) to 3.0 (♀) times longer than wide, elongate, longer than clavus, slightly contracted near base; disc with Y-shaped elevation; apex subtruncated or rounded; lateral margins emarginated.

Abdomen: Abdominal sternite II visible, slender, with medium sized conical tubercle close to lateral angle and near to metacoxae; abdominal sternite III expanded, in dorsal view with spiracle visible.

Male genitalia: Genital capsule simple, semiglobose; posteroventral edge with broad tongue-like middle plate, with small notch at middle third; lateral angles rounded. Paramere: Simple, straight; anterior lobe convex, continuous with body, apex ending in a slender projection with sharp apical tooth (Fig. 17).

Female genitalia: Plica narrowly, U-shaped; gonocoxae I squarish, in caudal view closed, in lateral view almost straight, upper border rounded. Spermatheca: Bulb somewhat elongate; spermathecal duct moderately coiled proximally, with two coiled distally; flank distinct; chamber more or less globose (Fig. 16).

Integument: Body surface densely covered with long to short decumbent to suberect hairs; head, calli, clavus, corium, prosternum, mesosternum, and metasternum impunctate; pronotum strongly punctate and abruptly striate; scutellum punctate, except lateral margin; propleura, posterior

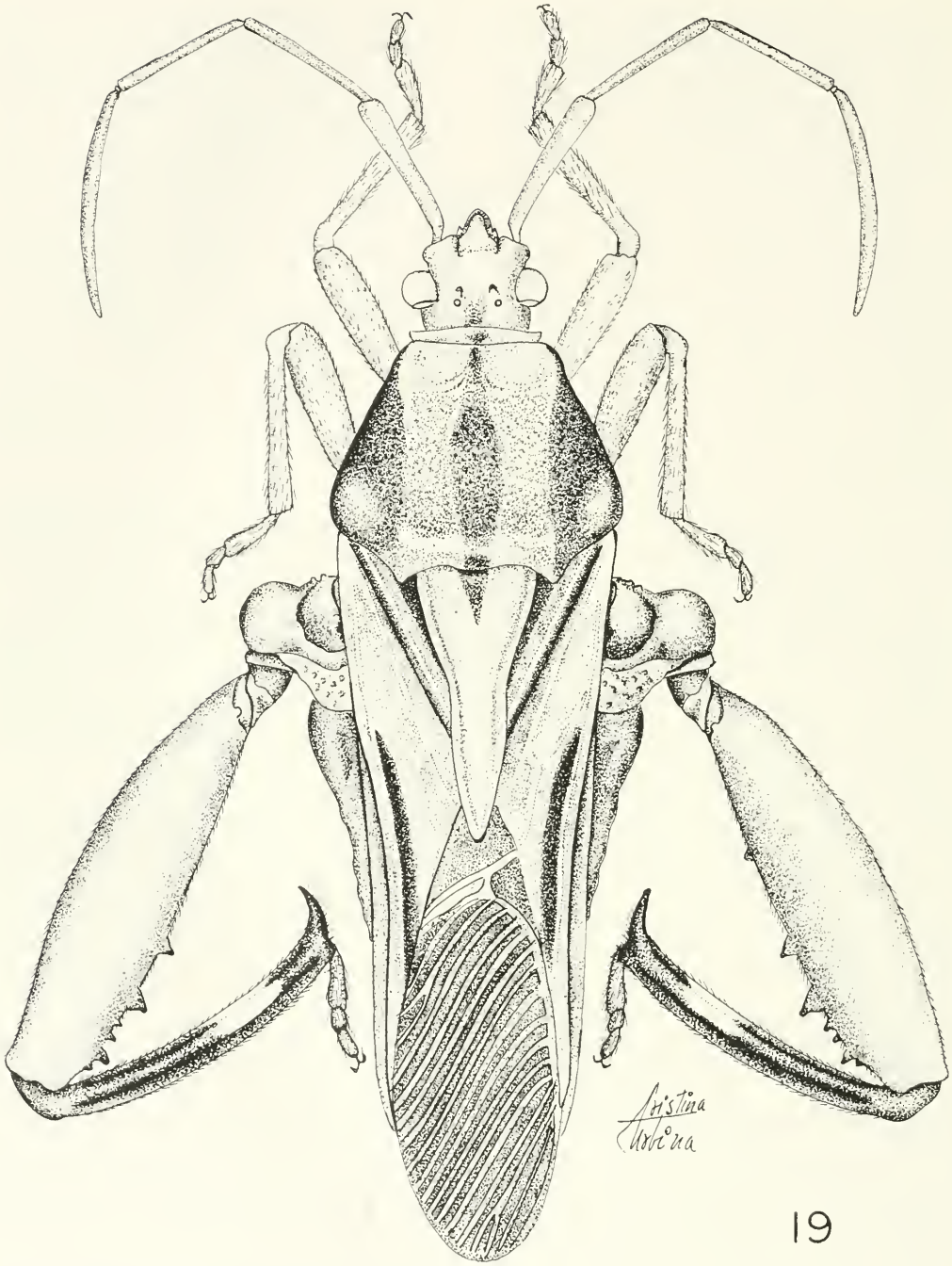


Fig. 19. Dorsal view of *Alcocerniella limonensis*.

margin of metapleura, acetabulae, and pleural abdominal sterna scarcely punctate; metapleura weakly tuberculate; antennal segments and legs densely covered with short decumbent to suberect setae; calli, pronotal disc, and abdominal sterna III with conspicuous creamy-yellow callosities like-tubercles or irregular spots.

Etymology.—Named for Eusebio Juaristi Cosio, distinguished Mexican chemist.

Type species.—*Juaristiella pacificae* Brailovsky, new species.

Juaristiella pacificae Brailovsky, new species

(Figs. 3, 7, 16–17, 20)

Description.—*Measurements:* Male: Head length 1.45; width across eyes 1.95; interocular space 1.17; interocellar space 0.51; distance ocellus to eye 0.21; diameter of ocellus 0.12; preocular distance 1.05; length antennal segments: I, 3.10; II, 2.50; III, 2.35; IV, 3.30; length rostral segments: I, 0.58; II, 0.55; III, 0.49; IV, 0.70. Pronotum: Total length 3.95; width across frontal angles 2.10; width across humeral angles 5.00. Scutellar length 4.25; maximum width of anterior lobe 2.00; maximum width of posterior lobe 1.32. Hind leg: femur length 7.52; tibia length 5.16. Total body length 17.52.

Female: Head length 1.35; width across eyes 1.87; interocular space 1.17; interocellar space 0.74; distance ocellus to eye 0.18; diameter of ocellus 0.15; preocular distance 1.00; length antennal segments: I, 2.60; II, 2.05; III, 2.00; IV, 3.00; length rostral segments: I, 0.65; II, 0.49; III, 0.46; IV, 0.68. Pronotum: Total length 3.70; width across frontal angles 2.05; width across humeral angles 4.70. Scutellar length 3.30; maximum width of anterior lobe 1.80; maximum width of posterior lobe 1.10. Hind leg: femur length 6.68; tibia length 4.78. Total body length 14.94.

Dorsal coloration: Male: Head bright chestnut orange; antennal segments I to III orange, and IV orange with red reflections; pronotum dirty orange with punctures pale brown, calli bright orange, following areas black: anterolateral borders including spines and tubercles, and a medial longitudinal stripe running from anterior to posterior margin; callosities of pronotal disc bright orange to creamy yellow; scutellum orange yellow with medial, and lateral longitudinal stripes reddish brown; clavus dark yellow orange with claval vein brown; corium dark yellow orange with brown longitudinal stripes between veins; hemelytral membrane dark ambarine, veins and basal angle reddish brown; connexival segments III to IV orange yellow, upper margin with short reddish brown longitudinal stripe, segment VII black with distal third dirty yellow; dorsal abdominal segments I to middle third of VI pale brown, abdominal scars IV–V and V–VI yellow; distal third of abdominal segment VI, and segment VII black. *Ventral coloration:* Head chestnut orange with medial longitudinal stripe black; rostral segments orange yellow with red reflections (apical third of IV red brown); prosternum pale brown; mesosternum chestnut orange, medial longitudinal stripe, and anterior tubercle pale reddish brown; metasternum bright dark reddish brown, medial longitudinal stripe bright chestnut orange; propleuron dirty yellow with punctures reddish brown, and a large anterior orange yellow callosity; mesopleuron reddish brown with two large orange yellow callosities; metapleuron reddish brown, posterior margin dirty yellow with brown punctures and three large orange yellow callosities; acetabulae dirty yellow with pale brown punctures; anterior and posterior lobes of metathoracic peritreme pale yellow; fore and middle legs chestnut orange; hind leg with coxa, trochanter, femur, and outer face of tibia bright reddish brown with tubercles of femur, and inner face and apical spine of tibia yellow to chestnut orange; tarsus chestnut orange to yellow; abdominal sterna III to VI dark chestnut orange with creamy yellow callosities on sterna III and IV; sternite VII dark chestnut orange, posterior third reddish brown; genital capsule reddish black with dark orange reflections; pleural margin of sterna III to VI yellow, VII black with apical third dirty yellow; spiracles creamy yellow.

Female: Similar to male. Connexival segments VIII and IX black, posterior angle pale orange yellow; abdominal segments VIII and IX black, lateral margins chestnut

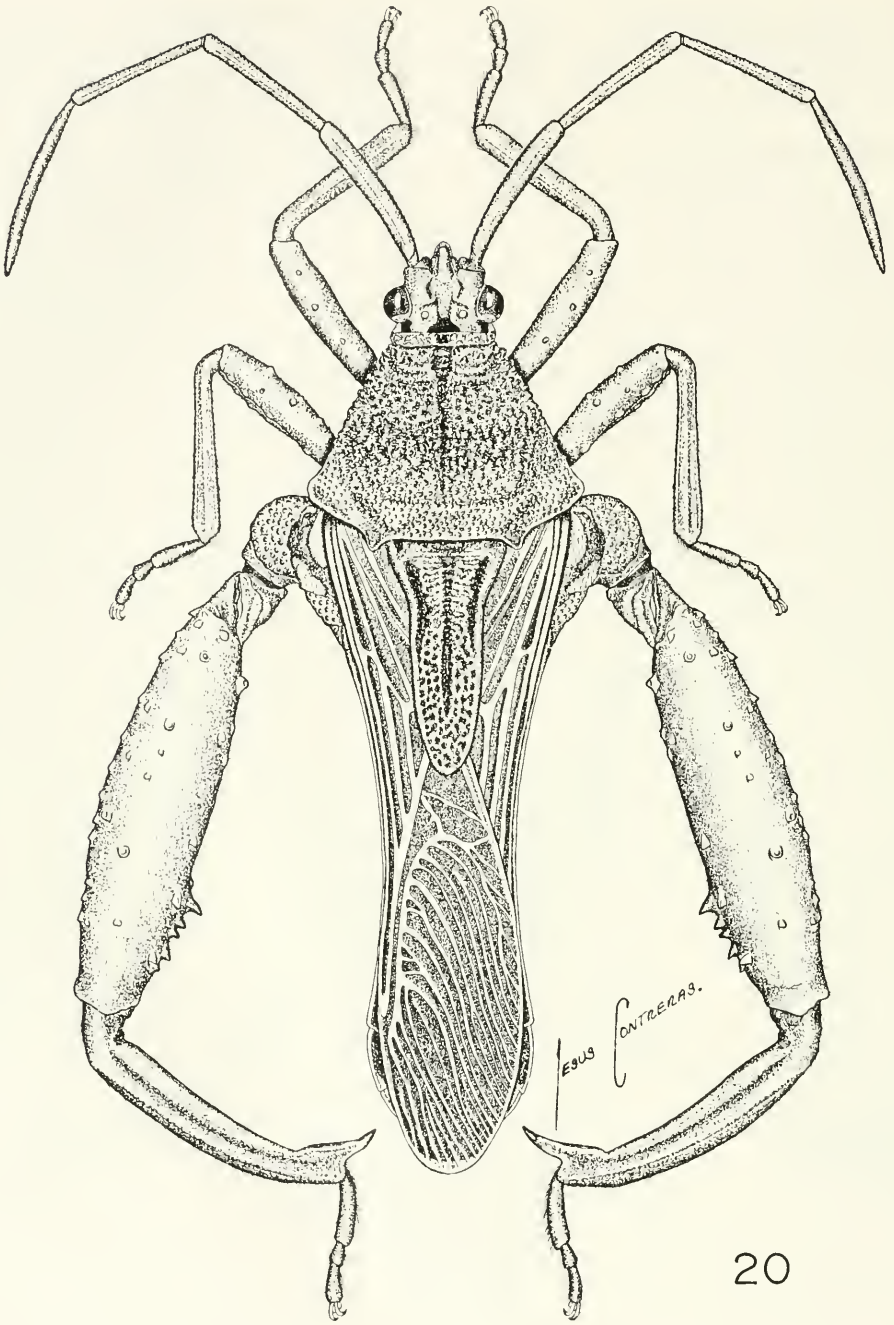


Fig. 20. Dorsal view of *Juaristiella pacificae.*

orange; genital plates orange yellow, external angle and inner face of gonocoxae I pale brown.

Variations in coloration: 1, Mesosternum chestnut orange, anterior and posterior tubercles bright reddish brown. 2, Metasternum bright orange yellow or bright chestnut orange, or bright reddish brown. 3, Antero-

lateral borders of pronotum dirty yellow, spines and tubercles black to reddish brown. 4, Outer face of hind tibia with anterior third bright reddish brown, posterior third yellow with or without reddish brown longitudinal stripes. 5, Abdominal sterna III and IV of female with or without creamy yellow callosities lateral to middle line.

Type material.—Holotype: ♂, Bolivia, Prov. Sara (without further data), Steinbach (AMNH). Paratypes: BOLIVIA: 1 ♂, 3 ♀ Prov. Sara (without data), Steinbach (AMNH, UNAM); 1 ♀, Jungas de la Paz (without data), V. Linnaea (ZMB); PERU: 2 ♀, Junjin, between San Ramon de Pangoa and Sonomoro, 40 km. SE Satipo (750 m), 10 January 1972, R. T. and J. C. Schuh (AMNH, UNAM); 1 ♂, Tingo Maria, Huanuco (700 m), July 1974, C. Bordon (UNAM); 1 ♂, 2 ♀, Tingo Maria, Monzon Valley, 12 October 1954, and 2 November 1954, E. I. Schlinger and E. S. Ross (CAS). 1 ♀, Ob Madre de Dios (500 m), V. Garlepp (ZMB); ECUADOR: 1 ♀, Prov. Napo, Tena (400 m), February 1983, M. Sharkey (UNAM).

Etymology.—Named for its occurrence in the Pacific slope.

Distribution.—Known only from the transandean slope including Ecuador, Peru, and Bolivia.

Larraldiella Brailovsky, new genus

Diagnosis.—*Larraldiella* like *Gracchus* share the following characters: head ventrally and behind buccula without tubercle, triangular process of pronotum absent, scutellum without Y-shaped elevation, dorsal surface of hind femur smooth, humeral angles subacute, mesosternum flat, lobes of posterior margin of mesosternum and anterior margin of metasternum remarkably small and in the same relative position, middle third of posterior margin of metasternum flat, without lateral lobes (Figs. 11–12).

In *Larraldiella* the scutellum conspicuously slender, metapleura not laterally expanded, hind femur relatively slender, inner face of hind tibia scarcely exposed, abdominal sternite III of the male has small lateral prominences, spiracle is not visible in dorsal view, and abdominal sternite VII of male not laterally expanded. Each of these characters are opposite in *Gracchus*, including the abdominal sternite III of the male being smooth, without lateral prominences or tubercles.

Generic description.—*Head:* Distance between ocelli 2.6 times the diameter of one ocellus; distance between ocellus to eye 1.6 to 2.0 times the diameter of one ocellus; head ventrally and behind buccula without tubercle; rostrum almost reaching middle third of mesosternum; rostral segment III shortest, IV equal than I, and longer than II.

Thorax: Pronotum: Humeral angles slightly projecting; anterolateral borders obliquely straight, smooth, emarginated; posterior border barely convex; triangular processes absent. Mesosternumm flat, anterior margin in front of area between fore legs produced into narrowed subacute tubercle, posterior margin between middle legs subelevated, bilobed, each lobe remarkably short, well separated from mesial line and in the same relative position as lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin with two small lobes, separated along midline by a wide furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum straight, lateral angles projected into broad rectangular plate, lying against metacoxae, and at middle third entirely flat (Fig. 11); lateral margin of mesopleura raised on a short tubercle, not overlapping posterior margin of propleura; metathorax laterally slightly expanded, in dorsal view with metapleura and acetabulae scarcely visible. Anterior lobe of metathoracic peritreme almost reniform (Fig. 5).

Legs: Hind coxa well separated, distance between them nearly 2.7 to 2.9 diameter of one coxa, outer apical angle scarcely tuberculate; hind trochanter convex; fore and middle femora relatively slender, unarmed;

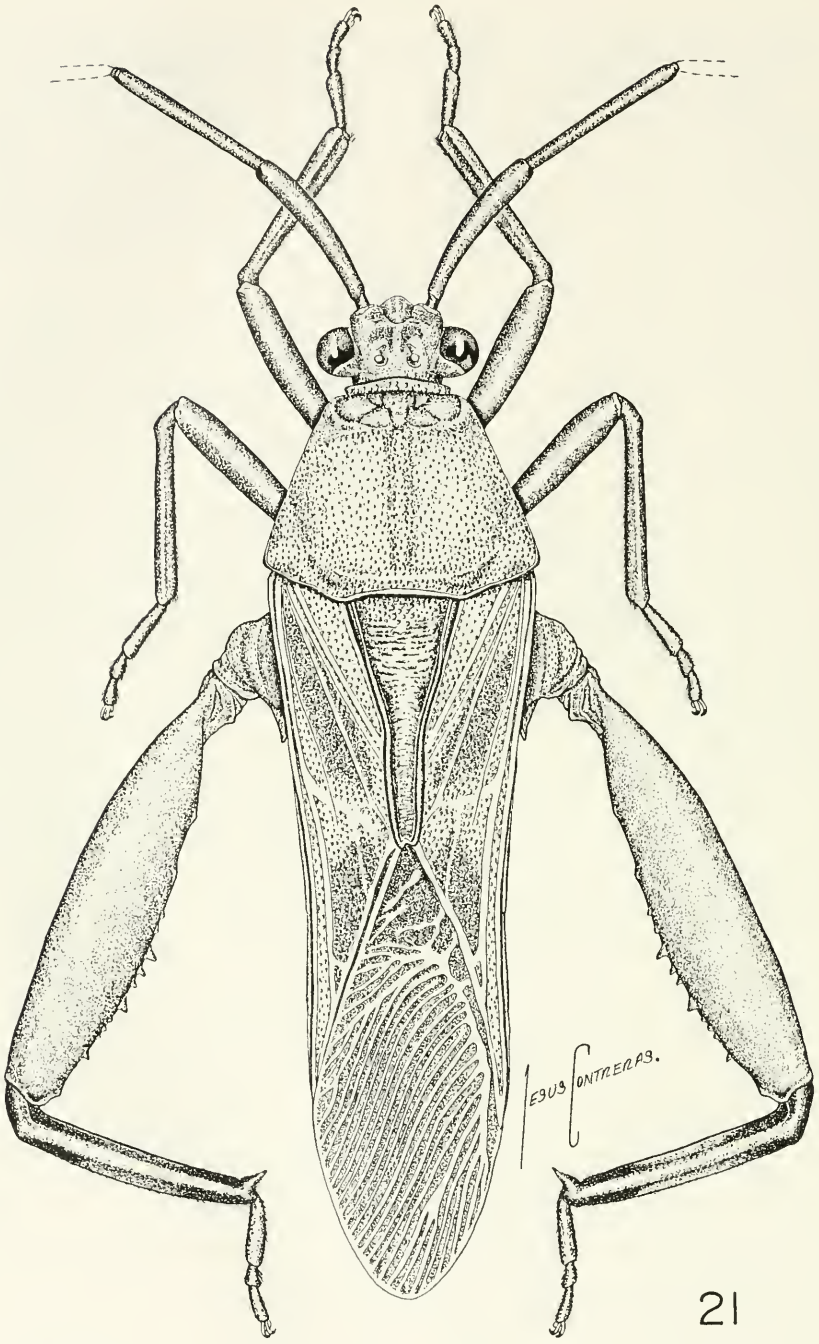


Fig. 21. Dorsal view of *Larraldiella terminalis*.

hind femur slightly incrassatte, almost attaining anterior margin of last abdominal sternite, dorsal surface smooth, ventrally armed with spines and tubercles in two irregular rows, without a strong tooth close to base; inner margin of hind tibia scarcely expanded, apically armed with a slender and relatively long spine.

Scutellum: 1.8 to 2.2 times longer than wide, elongate, clearly tringular, longer than clavus, not contracted near base; disc without Y-shaped elevation; apex bifid; lateral margins emarginated.

Abdomen: Abdominal sternite II visible, slender, without conical tubercle; abdominal sternite III clearly expanded, in dorsal view with spiracle not visible; male abdominal sternite III laterally produced into two small protuberances; female abdominal sternite III flat, without lateral prominences.

Male genitalia: Genital capsule simple, semiglobose; posteroventral edge entire, straight, with medial irregular plate, and laterally with angles rounded.

Integument: Dorsal surface almost glabrous, ventrally with few erect setae on mesosternum and abdominal sterna; head, calli, prosternum, mesosternum, metasternum, and abdominal sterna impunctate; pronotum strongly punctate, striate; scutellum with scattered punctures, striate, except lateral margins; clavus, corium, propleuron, posterior margin of metapleuron, and acetabulae punctate; metapleura not tuberculate; antennal segments and legs finely covered with short decumbent to suberect setae.

Etymology.—Named for Carlos Larralde Rangel, distinguished Mexican immunologist.

Type species.—*Larraldiella terminalis* Brailovsky, new species.

Larraldiella terminalis Brailovsky, new species

(Figs. 5, 11, 21)

Description.—*Measurements:* Male: Head length 1.16; width across eyes 1.92; interocular space 0.96; interocellar space 0.30; distance ocellus to eye 0.19; diameter of ocellus 0.12; preocular distance 0.74; length antennal segments: I, 2.08; II, 2.00; III and IV absent; length rostral segments: I, 0.62; II, 0.60; III, 0.37; IV, 0.62. Pronotum: Total length 2.56; width across frontal angles 1.84; width across humeral angles 3.28. Scutellar length 2.92; maximum width of anterior lobe 1.36; maximum width of posterior lobe 0.48. Hind leg: femur length 5.27; tibia length 2.91. Total body length 11.75.

Female: Head length 1.28; width across eyes 1.96; interocular space 1.08; interocellar space 0.32; distance ocellus to eye 0.24; diameter of ocellus 0.12; preocular distance 0.80; length antennal segments: I, 2.00; II, 1.96; III, 1.68; IV, 2.60; length rostral segments: I, 0.65; II, 0.62; III, 0.42; IV, 0.65. Pronotum: Total length 2.64; width across frontal angles 1.84; width across humeral angles 3.44. Scutellar length 2.60; maximum width of anterior lobe 1.40; maximum width of posterior lobe 0.44. Hind leg: femur length 5.20; tibia length 3.41. Total body length 11.77.

Dorsal coloration: Male: Head, antennal segments I and II (III and IV absent), pronotum and scutellum chestnut orange; clavus chestnut yellow, punctures reddish brown; endocorium pale red, exocorium chestnut yellow with punctures pale red; hemelytral membrane dark ambarine, veins and basal angle black; connexival segments III to V yellow, VI and VII yellow with anterior third bright orange; abdominal segments bright orange. *Ventral coloration:* Including rostral segments (apex of IV black), legs, metathoracic peritreme, and genital capsule pale yellow; hind tibia yellow with two reddish-brown rings, one basally the other distally.

Female: Similar to male. Antennal segments I to III chestnut orange, and IV dark reddish orange; scutellum basally with rounded chestnut orange spot near middle third; connexival segments III to VI yellow with anterior third or anterior half dark orange, and segments VII to IX dark orange; abdominal segments II to IX bright to dark orange; genital plates yellow.

Type material.—Holotype: ♂, Brazil, Amazonas, Manaus, 13 January 1956, Elias and Roppa (MNR). Paratypes: BRAZIL: 1 ♀, Amazonas, Manaus, 20 January 1956, and 8 November 1956, Elias and Roppa (MNR); 1 ♀, Amazonas, Humaita, August 1980, G. S. Andrade (UNAM).

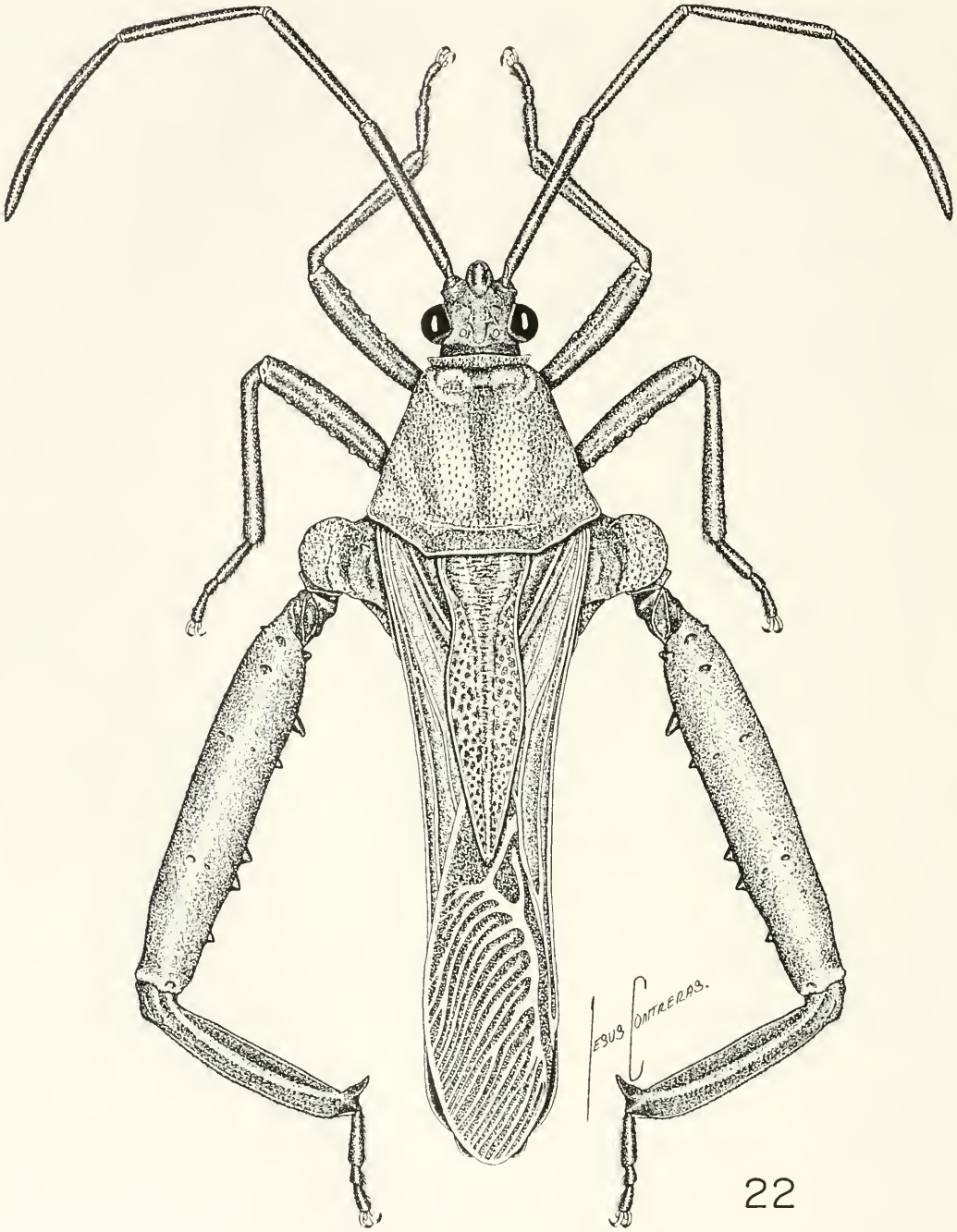


Fig. 22. Dorsal view of *Soteloniella perparvula.*

Etymology.—Named for the terminal section of the scutellum; from the latin, *Terminalis.*

Distribution.—Known only from Brazil.

***Possaniella* Brailovsky, new genus**

Diagnosis.—*Possaniella* Brailovsky new genus, and *Meropachys* Burmeister, are the

only known genera in the tribe Meropachydini that have the hind femur clavate, slender towards the base, and abruptly incrassate before midlength. The other genera have the hind femur uniformly incrassate. *Possaniella* shares with *Meropachys* the following additional characters: scutellum clearly contracted near the middle third, triangular process of pronotum broad, anterior margin of mesosternum conspicuously raised on a compressed tubercle, and posterior margin of metasternum flat, not bil.

Possaniella differs from *Meropachys* by the following characters: head ventrally and behind buccula strongly tuberculate, buccula almost quadrate, short, not extending beyond the antenniferous tubercles, posterior margin of mesosternum bilobed, anterior margin of metasternum bilobed, and pronotal disc without tubercles. In *Meropachys* the head ventrally and behind buccula without tubercle, buccula rectangular extending beyond antenniferous tubercles and reaching behind middle of head, posterior margin of mesosternum trilobed (Fig. 9), anterior margin of metasternum flat, and pronotal disc densely tuberculate.

Generic description.—*Head:* Distance between ocelli 5.0 times the diameter of one ocellus; distance between ocellus to eye 1.4 times the diameter of one ocellus; head ventrally and behind buccula strongly tuberculate; rostrum short, barely reaching anterior third of mesosternum; rostral segment III shortest, IV longest, I longer than II.

Thorax: Pronotum: Humeral angles obtuse, not projecting; anterolateral borders obliquely straight, smooth, not emarginate; posterior border barely straight, with triangular process broad, apically rounded. Mesosternum not raised, anterior margin in front between fore legs conspicuously raised into flat plate, posterior margin between middle legs prominent, bilobed, with each lobe well separated from mesial line and overlapping with lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin raised on two large lobes, separated along midline by a wide furrow; each lobe connected with the two lobes of posterior margin of mesosternum; posterior margin of metasternum almost straight, with lateral angles projected into broad rectangular plate, laying against metacoxae, at middle third entirely flat; lateral margin of mesopleura raised on an elongate tubercle overlapping posterior margin of propleura; metathorax laterally expanded, in dorsal view with metapleuron and acetabulae broadly visible. Anterior lobe of metathoracic peritreme hatchet-shaped.

Legs: Hind coxae well separated, distance between them nearly 4.2 times diameter of one coxa, with outer apical angle weakly tuberculate; hind trochanter convex; fore and middle femora relatively slender, ventrally with two irregular rows of tubercles; hind femur markedly clavate, slender towards base and behind middle abruptly incrassate, attaining posterior margin of abdominal sternite VI, dorsal surface with two rows of small tubercles, ventrally biseriately spined and tuberculate, without a strong tooth close to base; inner margin of hind tibia well expanded.

Scutellum: 1.8 times longer than wide, longer than clavus, clearly contracted near middle third; disc with short Y-shaped elevation restricted to basal half; apex rounded; lateral margins clearly emarginate.

Abdomen: Abdominal sternite II visible, slender, with conical tubercle close to hind coxae; abdominal sternite III clearly expanded, flat, without conical tubercles, in dorsal view with spiracle visible.

Integument: Body surface with short, uniformly decumbent to erect hairs; head, calli, clavus, corium, prosternum, mesosternum, metasternum and abdominal sterna impunctate; pronotum finely punctate, weakly striate; scutellum finely punctate, except lateral margins and Y-shaped elevation (arms of Y-shaped weakly striate); propleuron, posterior margin of metapleuron, and acetabulae finely punctate; metapleuron weakly tuberculate; antennal seg-

ments and legs densely covered with short decumbent to suberect setae.

Etymology.—Named for Lourival Domingos Possani Postay, distinguished Mexican biochemist.

Type species.—*Possaniella oblata* Brailovsky, new species.

Possaniella oblata Brailovsky, new species

(Fig. 23)

Description.—*Measurements:* Female: Head length 1.70; width across eyes 2.25; interocular space 1.25; interocellar space 0.62; distance ocellus to eye 0.18; diameter of ocellus 0.12; preocular distance 1.17; length antennal segments: I, 2.85; II, 2.25; III, 2.10; IV, 3.30; length rostral segments: I, 0.65; II, 0.62; III, 0.52; IV, 0.70. Pronotum: Total length 4.65; width across frontal angles 2.65; width across humeral angles 5.50. Scutellar length 4.35; maximum width of anterior lobe 2.40; maximum width of posterior lobe 1.80. Hind leg: femur length 7.60; tibia length 5.50. Total body length 16.50.

Dorsal coloration: Head included antennal segments I to IV bright chestnut orange; pronotum bright chestnut orange, posterior margin (except middle third and triangular process) and three irregular longitudinal stripes dark brown; scutellum with basal half chestnut orange, apical half dirty yellow, and both with a wide longitudinal medial stripe reddish brown; clavus black with vein yellow; corium dark brown with veins and apical half of costal border, dirty yellow; hemelytral membrane dark ambarine, veins and basal angle black; connexival segment III dark brown with posterior angle chestnut yellow, segments IV and V with anterior half dark brown and posterior half chestnut yellow, segment VI chestnut yellow with upper border dark brown, VII to IX dark brown; abdominal segments dark brown to black with scars IV–V and V–VI yellow. *Ventral coloration:* Included rostral segments I to IV and fore and middle legs chestnut orange with following areas black to reddish brown: apex of rostral segment IV, anterior tubercle and lateral margins of mesosternum, tarsi, area around metathoracic peritreme, middle third of metasternum, upper margin of hind acetabulae, abdominal sterna II and III, pleural abdominal margin III and anterior third of IV, posterior border of sterna V and VI, plica, posterior margin of sterna VII and great portion of genital plates; hind leg bright chestnut orange, spines, tubercles, two wide irregular rings on femur one distally the other close to middle third, and inner margin of tibia black.

Male.—Unknown.

Type material.—Holotype: ♀, Brazil, Santarem, July 1919, S. M. Klages (CMN).

Etymology.—Named for its obese shape; from the latin *oblatus.*

Distribution.—Known only from the type locality, Brazil.

Soteloniella Brailovsky, new genus

Diagnosis.—*Soteloniella* shares the following characters with *Marichisme:* head ventrally smooth, without conical tubercle behind buccula, triangular process on pronotum absent, posterior margin of mesosternum produced in two large lobes freely projecting backwards and bending up, not touching the anterior lobes of metasternum, and posterior margin of metasternum at middle third with deep capsule-like depression. In *Soteloniella* the scutellum is remarkably elongate, at least 3.3 to 3.8 times longer than wide and apically acute, anterior margin of thoracic mesopleuron without black spot, hind trochanter tuberculate, exposed, and dorsal surface of hind femur weakly tuberculate from base to middle third. In *Marichisme* the scutellum shorter, 1.7 to 2.2 times longer than wide and apically rounded, anterior margin of thoracic mesopleura with black elongate spot, hind trochanter slightly convex, not exposed, and dorsal surface of hind femur conspicuously tuberculate from base to apex.

Generic description.—*Head:* Distance between ocelli 2.4 to 3.0 times the diameter

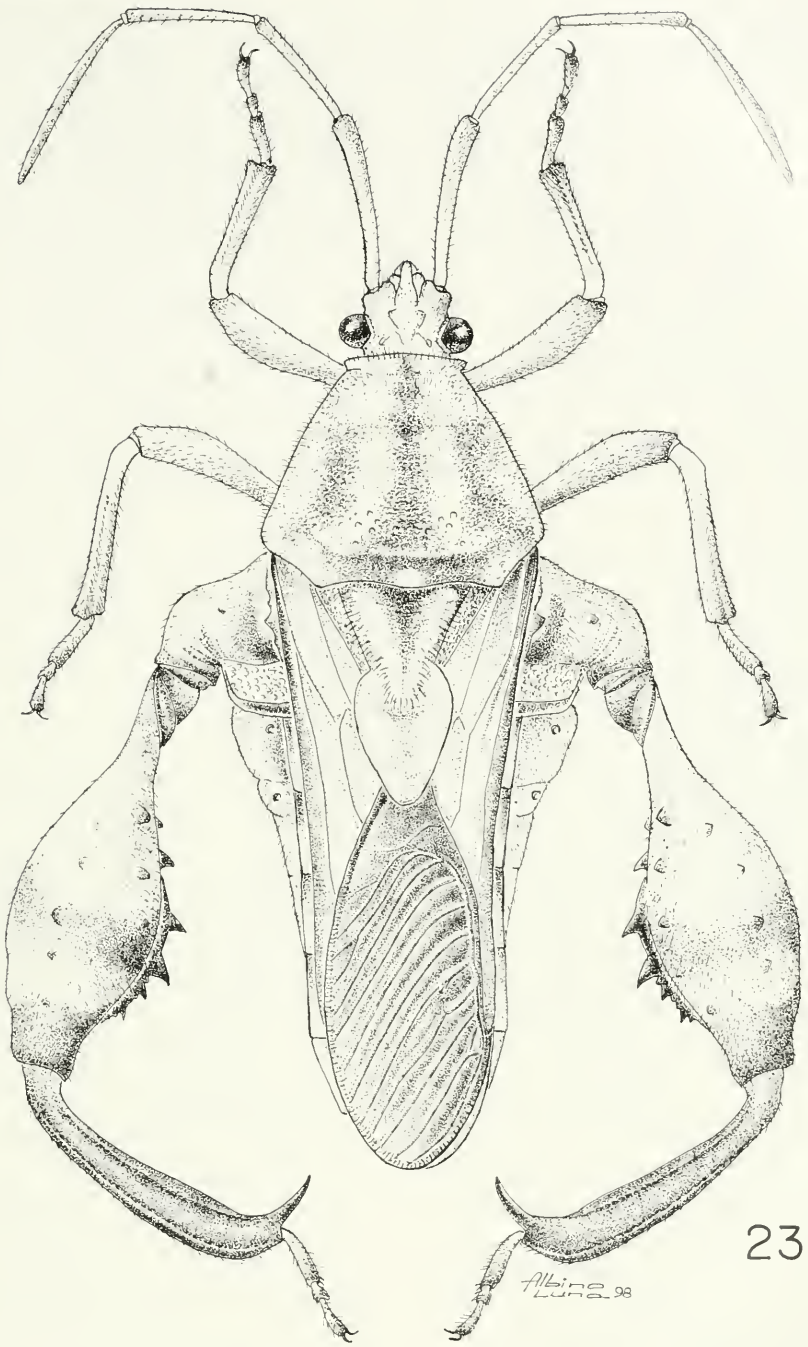


Fig. 23. Dorsal view of *Possaniella oblata.*

of one ocellus; distance between ocellus to eye 1.0 times or less the diameter of one ocellus; head ventrally and behind buccula without tubercle or with an irregular callosity; rostrum short, barely reaching anterior third of mesosternum; rostral segment III shortest, IV longest, I longer than II.

Thorax: Pronotum: Humeral angles

barely exposed; anterolateral borders obliquely straight, almost smooth, not emarginate; posterior border barely straight; triangular process absent. Mesosternum not raised, anterior margin in front of area between fore legs produced into narrowed subacute tubercle, posterior margin between middle legs prominent, bilobed, with each lobe well separated from mesial line and overlapping with lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin remarkably raised on two large lobes, separated along midline by a wide furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum almost straight, lateral angles projected into broad rectangular plate, lying against metacoxae, and at middle third with a deep hemispherical capsule-like depression (Fig. 13); lateral margin of mesopleura raised on a short elongate callosity; metathorax laterally expanded, in dorsal view metapleura and acetabulae remarkably visible. Anterior lobe of metathoracic peritreme vermiform, elongate, weakly curved upward (Fig. 2).

Legs: Hind coxae strongly separated, distance between them nearly 3.4 to 3.7 times the diameter of one coxa, with outer apical angle scarcely tuberculate; hind trochanter conspicuously projected on a wide and large tubercle; fore and middle femora relatively slender, armed with one to three subapical tubercles; hind femur markedly incrassate, not attaining apex of abdomen, reaching middle third of abdominal sternite VI, dorsal surface biseriately tuberculate from base to middle third or only basally, and ventrally strongly armed with spines and tubercles in two irregular rows, with a strong tooth close to the base; inner margin of hind tibia markedly expanded.

Scutellum: 3.3 to 3.8 times longer than wide, conspicuously elongate, lanceolate, longer than clavus, contracted near base; disc with Y-shaped elevation; apex subacute; lateral margins clearly emarginate.

Abdomen: Abdominal sternite II visible, slender, with or without conical tubercle located close to posterior border of metathorax; abdominal sternite III clearly expanded, in dorsal view with spiracle visible.

Male genitalia: Genital capsule simple, semiglobose; posteroventral edge entire, straight, lateral angles rounded.

Integument: Body surface with short decumbent to suberect hairs; head, calli, clavus, corium, prosternum, mesosternum, metasternum, and abdominal sterna impunctate; pronotum strongly punctate, abruptly striate; scutellum punctate, except lateral margins and Y-shaped elevation (arms of Y-shaped elevation finely punctate); propleuron, posterior margin of metapleuron, and acetabulae punctate; metapleuron weakly tuberculate; antennal segments and legs densely covered with short decumbent to suberect setae.

Etymology.—Named for Julio Sotelo Morales, distinguished Mexican neurologist.

Type species.—*Soteloniella scutellata* Brailovsky, new species.

Soteloniella scutellata Brailovsky, new species

Description.—*Measurements:* Male: Head length 1.60; width across eyes 2.20; interocular space 1.15; interocellar space 0.47; distance ocellus to eye 0.15; diameter of ocellus 0.17; preocular distance 1.07; length antennal segments: I, 3.75; II, 3.05; III and IV absent; length rostral segments: I, 0.77; II, 0.58; III, 0.53; IV, 0.80. Pronotum: Total length 4.30; width across frontal angles 2.50; width across humeral angles 5.00. Scutellar length 7.55; maximum width of anterior lobe 2.00; maximum width of posterior lobe 1.95. Hind leg: femur length 8.74; tibia length 4.78. Total body length 19.10.

Dorsal coloration: Head bright chestnut orange; antennal segment I with outer surface bright red orange, and inner face chestnut orange; segment II chestnut orange; pronotum orange yellow with punctures, space between calli, and lateral margin of callus bright red orange; scutellum yellow

with punctures and space between arms of Y-shaped elevation reddish brown to bright red orange; clavus and corium dark brown to dark orange with veins yellow; hemelytral membrane dark ambarine with veins and basal angle black; connexival segments III to VI with upper margin pale yellow and inner margin pale chestnut orange, and VII black; abdominal segments I to VI pale orange yellow, and VII black. *Ventral coloration:* Including rostral segments (apex of IV black) and metathoracic peritreme chestnut orange, with mesosternum and posterior margin of abdominal sternite VII bright to dull black; lateral margin of mesosternum, metasternum, and abdominal sternite II bright red orange; following areas yellow: irregular spots on propleuron, posterior margin and lateral margin of mesopleuron, posterior margin of metapleuron, and pleural margin of abdominal sterna II to VII; fore and middle legs dark orange yellow, and hind leg with coxae chestnut orange, trochanter bright reddish brown, femur and tarsi bright chestnut orange, and tibia bright black to reddish black.

Female.—Unknown.

Type material.—Holotype: ♂, Brazil, Kollur Bolioto, 3 October 1975 L. P. Albo and J. B. Moraes (UNAM).

Etymology.—The specific epithet refers to the remarkably developed scutellum.

Distribution.—Known only from the type locality, Brazil.

Soteloniella perparvula Brailovsky, new species

(Figs. 2, 13, 22)

Description.—*Measurements:* Male: Head length 1.50; width across eyes 2.05; interocular space 1.10; interocellar space 0.45; distance ocellus to eye 0.16; diameter of ocellus 0.14; preocular distance 1.00; length antennal segments: I, 3.45; II, 2.80; III, 2.75; IV, 4.55; length rostral segments: I, 0.68; II, 0.58; III, 0.51; IV, 0.77. Pronotum: Total length 3.60; width across frontal angles 2.10; width across humeral angles 4.00. Scutellar length 5.04; maximum width of anterior lobe 1.65; maximum width of posterior lobe 1.30. Hind leg: femur length 6.90; tibia length 4.40. Total body length 16.10.

Dorsal coloration: Head and pronotum chestnut orange; space between calli and lateral margin of each callus reddish orange; antennal segment I with outer surface bright red orange and inner face bright chestnut orange; segments II to IV bright reddish orange; scutellum bright chestnut orange, space between arms of Y-shaped elevation bright reddish orange; clavus and corium dark brown to dark orange, veins yellow; hemelytral membrane dark ambarine, veins and basal angle black; connexival segments III to VI orange yellow, VII black; abdominal segments I to basal half of V pale orange; distal half of V and VI dark orange, VII darker; abdominal scars IV–V and V–VI pale yellow. *Ventral coloration:* Including rostral segments (apex of IV black) and metathoracic peritreme bright orange yellow; following areas bright red orange: lateral margin of mesosternum, upper margin of hind acetabulae, metasternum, and posterior margin of genital capsule (lateral margin of genital capsule pale yellow orange); fore and middle legs pale orange yellow; hind leg with coxa, trochanter, femur and tarsus chestnut orange; hind tibia with inner and outer margins reddish brown, and middle third with ventral face bright orange and dorsal face bright orange with pale yellow ring.

Female.—Unknown.

Type material.—Holotype ♂, Brazil, Amazonas, Tefé, 27–31 July 1956, M. Alvarenga (MNR). Paratype, BRAZIL: 1 ♂, Amazonas, Manaus, 4 November 1955, Elias and Roppa (UNAM).

Etymology.—Named for its small size, the smallest known species of the genus.

Distribution.—Known only from Brazil.

Key to The Species of *Soteloniella*

1. Dorsal surface of hind femur strongly biseriately tuberculate from base to middle third; abdominal sternite II without lateral conical tu-

bercle close to posterior margin of metathorax; hind tibia entirely bright black to bright reddish black; body size longer than 19.00 mm; total length of scutellum longer than 7.20 mm . . . . . *Soteloniella scutellata*, n. sp.

— Dorsal surface of hind femur only weakly biseriately tuberculate basally; abdominal sternite II with large conical tubercle close to posterior border of metathorax; hind tibia not entirely bright black to bright reddish black; body size shorter than 16.20 mm; total length of scutellum shorter than 5.20 mm (Fig. 22) . . . . . *Soteloniella perparvula*, n. sp.

Peranthus Stål

Peranthus Stål 1867: 536
Menardus Distant 1900: 366. **New synonym.**

Walker (1871) included in the genus *Meropachys* one new species *notatus* collected in Brazil. Years later Distant (1900) described the genus *Menardus* to include *notatus* with the binomial *Menardus notatus* (Walker) comb. nov. Examination of the male lectotype of *Meropachys notatus* deposited in BMNH, as well as the male lectotype of *Peranthus longicornis* deposited in BMNH, and the male holotype of *Peranthus virescens* (Erichson) deposited in ZMB, shows that both genera are the same, and, for that reason, *Menardus* is here synonymized under *Peranthus*. The species *Menardus notatus* is thus transferred to *Peranthus* and the **new combination** *Peranthus notatus* (Walker) results.

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NEW CRANE FLIES (DIPTERA: LIMONIIDAE) FROM DOMINICAN AMBER

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Abstract.—Ten new species of crane flies including ***Dicranomyia fera, Dicranomyia lema, Gnophomyia ieva, Gnophomyia martyni, Gonomyia asymmetrica, Polymera specula, Polymera virgo, Rhipidia mira, Styringomyia dominicana,*** and ***Trentepohlia agri,*** (Diptera: Limoniidae) are described from Dominican amber.

Key Words: Dominican amber, *Dicranomyia, Gnophomyia, Gonomyia, Polymera, Rhipidia, Styringomyia, Trentepohlia*

Crane flies from Dominican amber have been little investigated. Krzeminsky (1992) examined 18 specimens in the American Museum of Natural History, New York, and 34 specimens in the Smithsonian Institution, Washington, D. C. Thus far, the only species described has been *Molophilus (Miomolophilus) theischingeri* Krzeminski, 1992. This study describes species from the Poinar collection (36 specimens), maintained at Oregon State University, Corvallis, and from the collection of the Academy of Natural Sciences in Philadelphia (2 specimens; designated ANSP).

MATERIALS AND METHODS

These specimens are believed to have originated from mines in the Cordillera Septentrional of the Dominican Republic. These mines are in the El Mamey Formation (Upper Eocene), which is a shale-sandstone interspersed with a conglomerate of well-rounded pebbles (Eberle et al. 1980). The exact age of the amber is unknown. While estimates based on foraminifera indicated a range of 15–20 million years (Iturralde-Vincent and MacPhee 1996), studies with coccoliths provided an upper range of 30–45 million years (Cepek 1990). Earlier studies with nuclear magnetic resonance gave an estimated range of 15–40 million years depending on the mine source (Lambert et al. 1985). Unfortunately, mine locality data of most specimens in this study were not available.

In the following descriptions, genitalia terminology and wing venation follows that presented in the "Manual of Nearctic Diptera" (McAlpine 1981). Thus *m-cu* and CuA_1 are considered separate veins. Occasionally cross-vein *r* is used to show the position of R_2 in relation to the longitudinal wing axis. Accession numbers pertaining to specimens in these collections are presented under the section "examined material."

Abbreviations used in the drawings are: *a*—aedeagus; CuA_2—anterior branch of cubitus; *dm*—discal medial cell; *gon*—gonocoxite; *i g*—inner gonostylus; *M*—media vein; *m-cu*—medial cubital cross vein; *o g*—outer gonostylus; *pm*—paramere; R_1—first branch of radius vein; R_2—second branch of radius vein; R_{2+3}—combined second and third radial veins; Sc_1—first subcoast vein; Sc_2—second subcosta vein. We have used the *r* cross vein here to represent

a cross vein connecting R_1 with R_2 or one of the other radial sector veins.

HEXATOMINAE

Polymera (Polymera) specula Podenas and Poinar, new species
(Figs. 1–3)

Diagnosis.—General body coloration grayish brown. Antennae much longer than body. Macrotrichiae of moderate length on all longitudinal veins. Genitalia dark brown. Outgrowth of ninth tergite very long and narrow, more than half as long as gonocoxites; cross-vein *m-cu* situated before fork of *M*; cross-vein *r* distant from tip of R_1.

Male.—Body length 3.05 mm, wing length 3.5 mm. Head, rostrum and antenna brown, the latter much longer than body; palpi covered with comparatively long bristles. Antenna (Fig. 3)16-segmented, about 4.7 mm long; scape twice as long as wide; pedicel spherical, about half length of scape; postpedicel or first flagellar segment longer than both basal segments together; all flagellar segments elongate, slightly nodulose; flagellum with verticils about as long as respective segments; apical segment nearly as long as preceding segment.

Thorax brown, with dark brown lateral stripes. Coxae and trochanters brown; remainder of legs missing. Wing clear, brownish, without any darker marks. Venation typical for genus (Fig. 1): Sc_1 ending at level of *Rs* fork, Sc_2 near its tip; *Rs* more than four times as long as R_{2+3}, arcuated; *r* distinct; basal section of R_2 about equal to terminal section of R_1; *m-cu* shortly before fork of *M*; discal medial cell absent. Macrotrichiae on all longitudinal veins. Halter brown.

Abdomen brown. Genitalia dark brown (Fig. 2). Outgrowth of ninth tergite long and narrow.

Female.—Unknown.

Examined material.—Holotype ♂, specimen number D-7-204, deposited in the Poinar collection.

Discussion.—This new species is most similar to *P. minutior* Alexander 1942 (known only from southern Ecuador) but differs from the latter by possessing a shorter *Sc* and Sc_2 being opposite the fork of *Rs*.

Polymera (Polymera) virgo Podenas and Poinar, new species
(Figs. 4–6)

Diagnosis.—General body coloration brown. Size comparatively large. Antennae much longer than body. Outgrowth of ninth tergite distally rounded; closed discal cell.

Male.—Body length 3.8 mm, wing length 4.3 mm. Head, rostrum and antenna brown; palpi lighter, covered with short hairs. Both antennae lacking 3 apical segments (Fig. 4); scape nearly twice as long as wide; pedicel spherical, about half length of scape; postpedicel or first flagellar segment more than twice as long as both basal segments together; flagellar segments elongated, slightly nodulose; flagellum with verticils longer than respective segments.

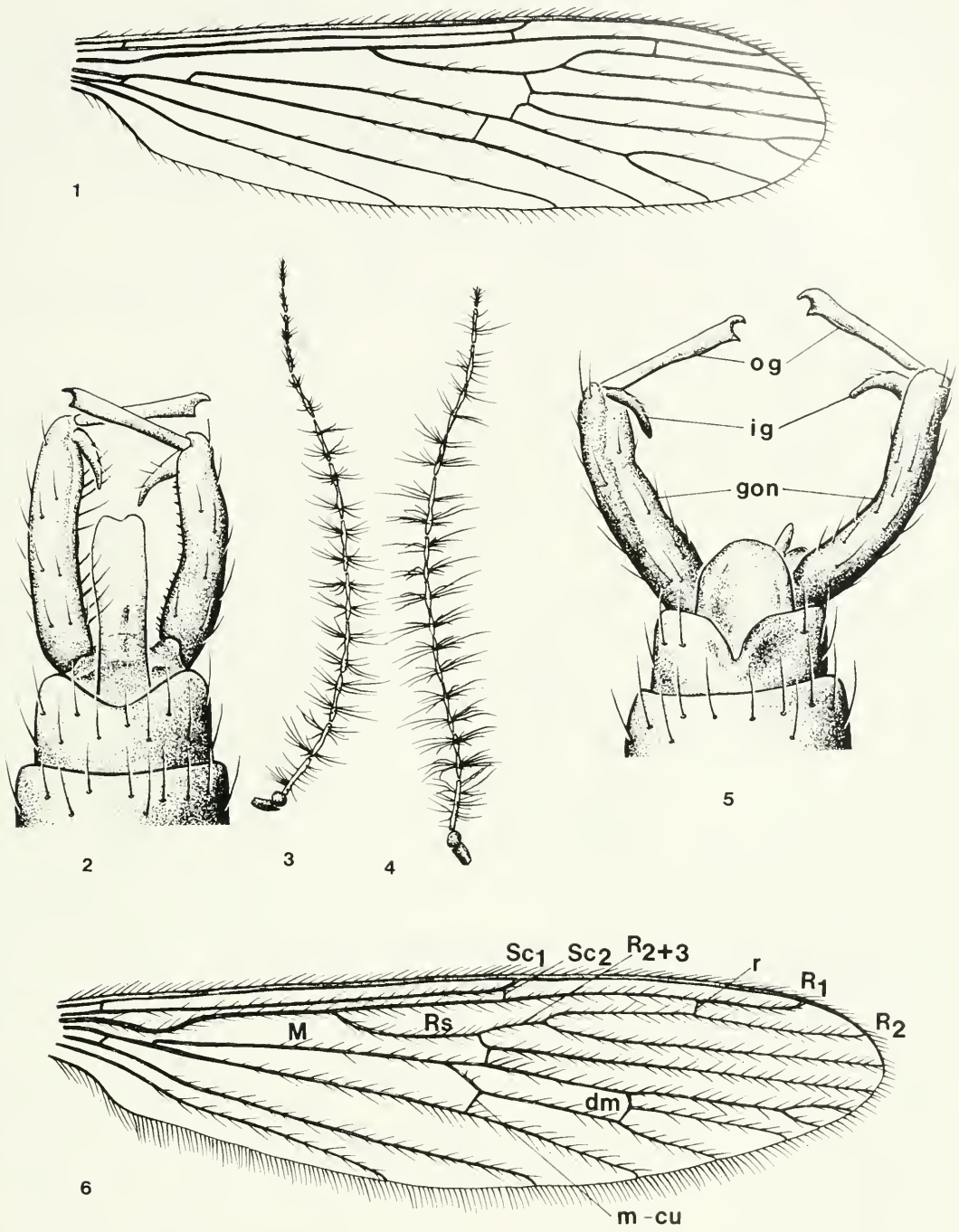
Thorax brown, with dark brown lateral bands. Legs brown. Femur 2: 3.2 mm, tibia 2: 3.3 mm (fore and hind legs missing). Wing clear, light brownish, without darker marks. Venation (Fig. 6): Sc_1 ending beyond level of *Rs* fork, Sc_2 near its tip; *Rs* twice as long as R_{2+3}, arcuated; *r* distinct; terminal section of R_1 about two thirds length of basal section of R_2; *m-cu* shortly beyond fork of *M*; discal medial cell present (unusual for genus). Macrotrichiae on all longitudinal veins. Stem of halter light brownish, knob slightly darker.

Abdomen brown. Genitalia same color as abdomen, details evident from Fig. 5. Outgrowth of ninth tergite distally rounded.

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-205, deposited in the Poinar collection.

Discussion.—The only recent species of *Polymera* with closed discal cells are *P. clausa* Alexander 1939 (from Ecuador) and *P. neoclausa* Alexander 1967 (from Honduras). Both of these extant species are nearly twice the size of *P. virgo* and the Sc



Figs. 1–6. 1–3, *Polymera* (*Polymera*) *specula,* holotype. 1, Wing. 2, Male genitalia, dorsal view. 3, Antenna. 4–6, *P.* (*P.*) *virgo,* holotype. 4, Antenna without tip. 5, Male genitalia, dorsal view. 6, Wing. (See Materials and Methods for abbreviations.)

vein of *P. virgo* is intermediate in length between those of *P. clausa* and *P. neoclausa*.

Polymera sp.
(Fig. 7)

Diagnosis.—General body coloration brown. Size comparatively large. Antennae much longer than entire body. Outgrowth of ninth tergite elongate and rounded at tip.

Male.—Body length 3.75 mm. Head, rostrum and antenna brown; palpi brown, covered with short hairs. Antenna 16-segmented, about 5.3 mm long; scape nearly as long as wide; pedicel spherical, about half length of scape; postpedicel or first flagellar segment three times as long as both basal segments together; all flagellar segments elongate, slightly nodulose; flagellum with verticils longer than respective segments; apical segment nearly as long as preceding segment.

Thorax brown, with dark brown lateral bands, prescutum with dark median stripe. Coxae and trochanters brown. Fore leg yellowish brown with darker femur, mid leg with dark brown femur, tibia lighter brown with dark brown apex, tarsus light brown with darker apical segment and tip of previous segment. Femur 1: 3.25, 2: 3.3 mm, tibia 1: 3.7, 2: 3.6 mm (posterior legs missing). Only bases of wings preserved, clear, whitish, with darker pigmentation along veins. Stem of halter brownish, knob brown.

Abdomen brown. Genitalia dark brown. Outgrowth of ninth tergite elongate (Fig. 7).

Female.—Unknown.

Examined material.—♂, number D-7-203, deposited in the Poinar collection.

Discussion.—This species differs from the others by the shape of the ninth tergite and antennae, but since nearly all the wings and apices of the terminalia are missing, there are not enough features to describe it as new, and it is not clear whether this species belongs to the subgenus *Polymera* Wiedemann, 1820.

Recent crane flies, belonging to the subgenus *Polymera* distributed in the Antilles are: *P. albitarsis albitarsis* Williston, 1896; *P. albitarsis dominicae* Alexander, 1926; *P. arawak* Alexander, 1964; *P. cavernicola* Alexander, 1964; *P. geniculata geniculata* Alexander, 1915; *P. geniculata pallipes* Alexander, 1964 (Alexander, 1970).

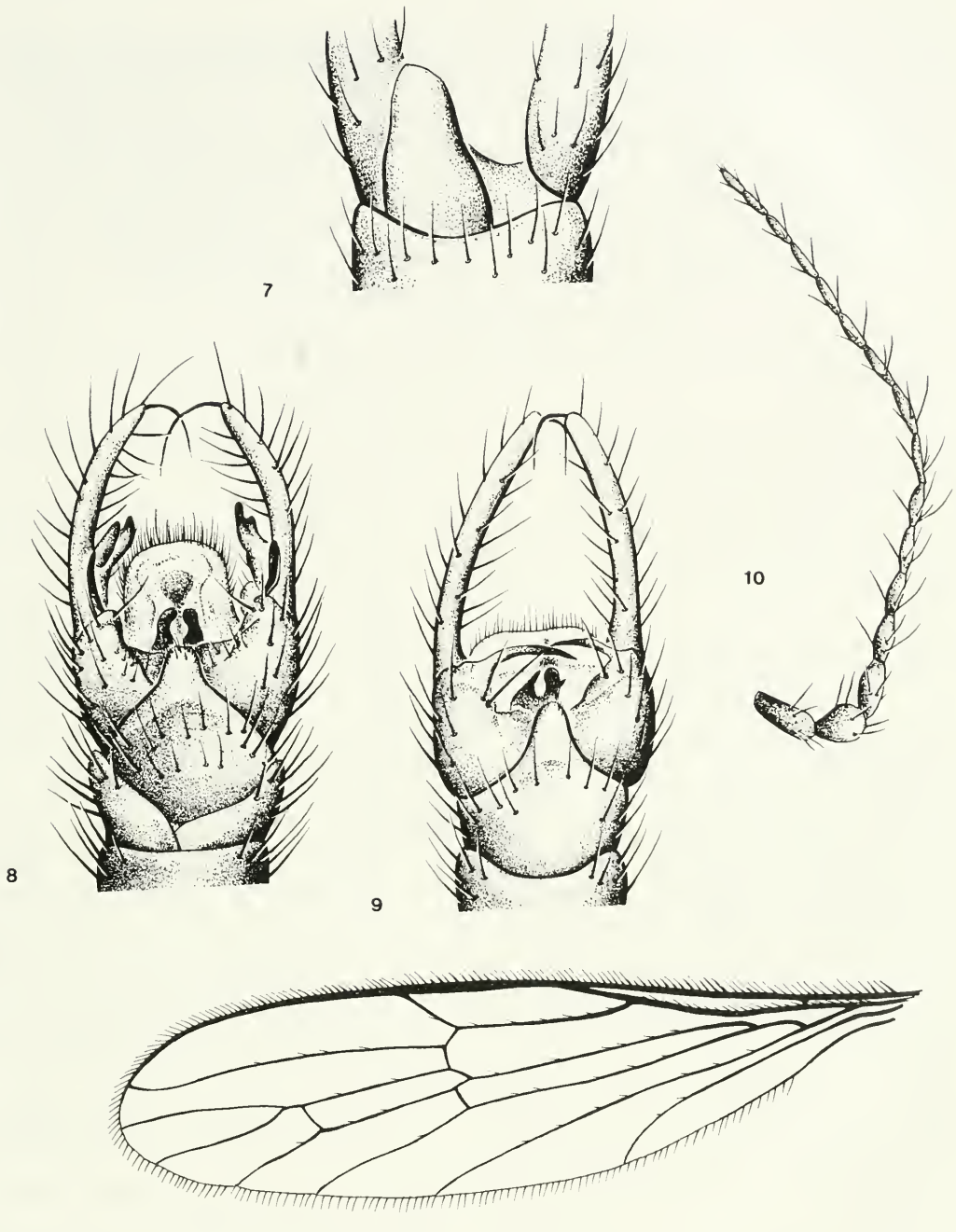
Eriopterinae

***Styringomyia dominicana* Podenas and Poinar, new species**
(Figs. 8–11)

Diagnosis.—Small species with short wings. General body coloration yellowish brown. Head, body and legs covered with long stout bristles. Legs comparatively short. Male genitalia with short gonocoxites and long gonostyli which separates this species from all other members of the genus.

Male.—Body length 5.9 (holotype)–7.1 (paratype) mm; wing length 3.9 mm. Head brownish; rostrum yellowish brown, palpi covered with long, brown, strong bristles (from one third to half length of respective segment). Antenna (Fig. 10) 16-segmented, yellowish, 1.3 mm long; scape twice as long as wide; pedicel pyriform, about two-thirds length of scape; postpedicel or first flagellar segment comparatively short, nearly same length as pedicel, but more slender; all flagellar segments elongated, apical segments nearly cylindrical; flagellum with verticils about length of respective segments; apical segment nearly as long as preceding segment.

Dorsal part of thorax yellowish brown, prothorax large compared to meso and metathorax; prescutum with two brown lateral stripes (median stripe can be discolored), pleura with brown marks, (which may have been formed during oxidization in amber). Coxae, trochanters and rest of legs yellowish brown with tips of tibiae brown. Wing clear, without any darker marks. Venation as usual for genus (Fig. 11): very short vein *R*, not reaching mid-length of wing; radial sector (*Rs*) with only two apical branches; discal medial cell very



Figs. 7–11. 7, *Polymera* sp., part of male genitalia, dorsolateral view. 8–11, *Styringomyia dominicana*. 8–9, Male genitalia, dorsal view. 8, Holotype. 9, Paratype. 10, Antenna, paratype. 11, Wing, holotype.

long and narrow, cell m_1 with short petiole, cross-vein *m-cu* distal to base of discal medial cell. Halter brownish.

Abdomen and genitalia brownish, details evident from Figs. 8, 9 (some details of dististyles not seen in paratype).

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-202, deposited in the Poinar collection.

Paratype ♂, number D-7-202A, deposited in the Poinar collection. Tips of wings and legs missing.

Discussion.—The genus *Styringomyia* Loew, 1845 was previously unknown from the Greater Antilles (Alexander 1970). This may be due to insufficient collections from this region. Recent species are found in Central and South America (Alexander 1970).

Gnophomyia ieva Podenas and Poinar, new species

(Figs. 12–14)

Diagnosis.—This is one of the smallest *Gnophomyia* species known; general body coloration brown; gonostyli long, slender and curved: inner gonostyli short and hooked apically, outer gonostyles longer, with basal portion enlarged and bearing a huge hook at their apices; separated from all other species by the Sc_2 far removed from the tip of Sc_1, the position of *m-cu* close to the fork of *M* and structure of the male genitalia.

Male.—Body length about 2.3 mm, wing length 2.5 mm. Head, rostrum, palpi and antenna yellowish brown. Antenna (Fig. 14) 16-segmented, 0.55 mm long; scape short, only 1.4 times as long as wide; pedicel pyriform, 1.7 times as long as scape; postpedicel or first flagellar segment short, subspherical, other flagellar segments ranging from elongate-oval to cylindrical, with conspicuous verticils that exceed segments in length; apical segment short, about half length of preceding segment.

Thorax brown; pleura lighter with indistinct longitudinal dark stripe. Legs yellowish brown; tips of femora yellow with a rather broad, dark subterminal ring. Femur 1: 1.4, 2: 1.5, 3: 1.95 mm, tibia 2: 1.5, 3: 2.0 mm, tarsus 2: 1.45, 3: 1.4 mm. Wing subhyaline, brownish. Venation usual for genus (Fig. 12): Sc_1 relatively elongate, ending just before *r*, Sc_2 far removed from tip of Sc_1, about opposite one-third length of *Rs*, Sc_1 thus about three-fourths length of *Rs*; *r* about twice its own length beyond origin of R_2 and far from tip of R_1; distal section of R_1 about three-fourths length of *Rs*; discal medial cell narrow, about 3.1 times as long as wide; crossvein *m-cu* slightly beyond fork of *M*. Halter brownish yellow, 0.35 mm long.

Abdomen and genitalia brown, details evident from Fig. 13; inner and outer gonostyli hooked apically.

Female.—Generally similar to male; body and head with long conspicuous hairs, body 3.3 mm long. Head light brown with dark brown vertex; rostrum dark basally, lighter distally; palpi yellowish brown, 0.3 mm long; antenna with brown basal segments and yellowish brown flagellum, 1.0 mm in length.

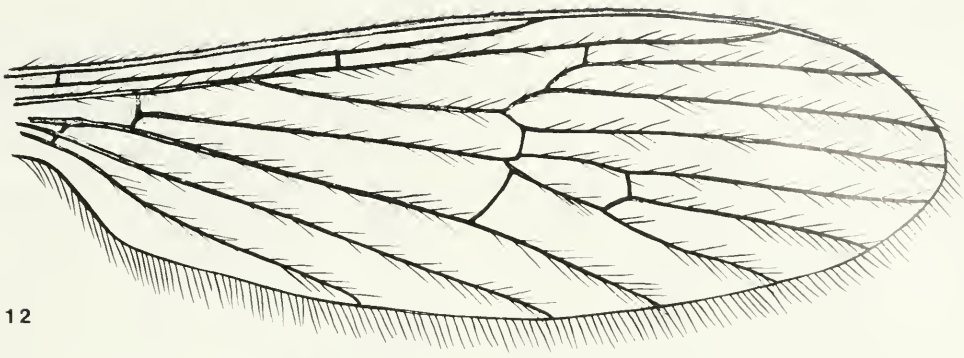
Thorax brown dorsally; pleura lighter with indistinct darker longitudinal stripe. Coxae, trochanters and rest of legs light brown with only tips of femora darker. Femur 1: 1.9 mm, tibia 1: 2.4 mm. Wing length 2.7 mm. Halter brownish yellow, 0.3 mm long, stem lighter, knob slightly darker.

Abdomen brown. Ovipositor brownish yellow.

Examined material.—Holotype ♂, number D-7-198, deposited in the Poinar collection.

Paratype ♀, number D-7-198A, deposited in the Poinar collection.

Discussion.—Similar long and slender gonostyles occur in *G. distifurcula* Alexander 1943 and *G. kertesziana* Alexander 1929, but both of these species have the shape of the ninth tergite and wing venation different (Sc_2 not far removed from Sc_1 tip and *m-cu* distant to fork of *M*) from that of *G. ieva*.



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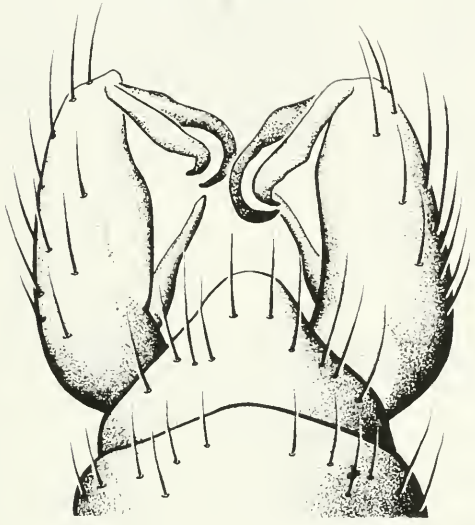

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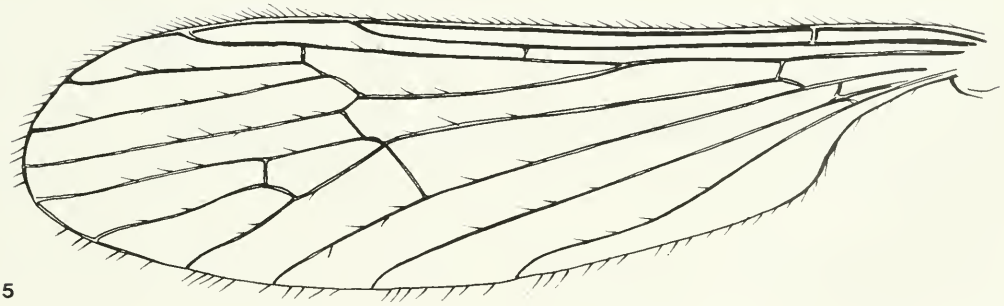

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Figs. 12–15. 12–14, *Gnophomyia ieva*, holotype. 12, Wing. 13, Male genitalia, dorsal view. 14, Antenna. 15, *G. martyni*, holotype, wing.

Gnophomyia martyni Podenas and Poinar, new species

(Figs. 15–17)

Diagnosis.—This is one of the smaller species of *Gnophomyia*. General coloration yellowish brown; Male genitalia with bluntly terminated ninth tergite and long slender gonostyli, including a deeply bifurcated outer gonostylus.

Male.—Body length 2.4 mm, wing length 2.8 mm. Head yellowish brown with darker vertex; rostrum and palpi yellowish brown. Antenna (Fig. 17) 16-segmented, basal two segments yellowish brown, flagellum yellow; scape short, nearly as long as wide; pedicel oval, twice as long as scape; first flagellar segment very short, oval, other flagellar segments ranging from elongate-oval to cylindrical, with conspicuous verticils that exceed segments in length; apical segment long, only slightly shorter than preceding segment.

Thorax yellowish brown dorsally; pleura whitish yellow with longitudinal dark stripe. Coxae, trochanters and rest of legs yellowish brown. Femur 1: 1.8, 3: 2.1 mm, tibia 1: 2.1, 3: 2.4 mm, tarsus 1: 2.1, 3: 1.5 mm. Wing without any dark marks. Venation as usual for genus (Fig. 15): Sc_1 relatively elongate, ending before *r*, Sc_2 very far removed from tip of Sc_1, about opposite one-third length of *Rs*, Sc_1 about two thirds length of *Rs*; *r* about 1.5 times its own length beyond origin of R_2 and far from tip of R_1; distal section of R_1 being less than half length of *Rs*; discal medial cell narrow, about three times as long as wide; crossvein *m-cu* joining fork of *M*. Halter yellow, 0.5 mm long.

Abdomen and genitalia yellowish brown; details of genitalia as in Fig. 16; outer arm of outer gonostylus straight, inner arm curved inward, inner gonostylus straight.

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-199, deposited in the Poinar collection.

Discussion.—Both new fossil species of *Gnophomyia* Osten Sacken, 1859, differ from extant species by the position of vein Sc_2, which is far removed from the end of Sc_1. Only *G. diazi* Alexander, 1937, occurs at present in the Antilles (Puerto Rico).

Gonomyia (Paralipophleps) asymmetrica Podenas and Poinar, new species

(Figs. 18–20)

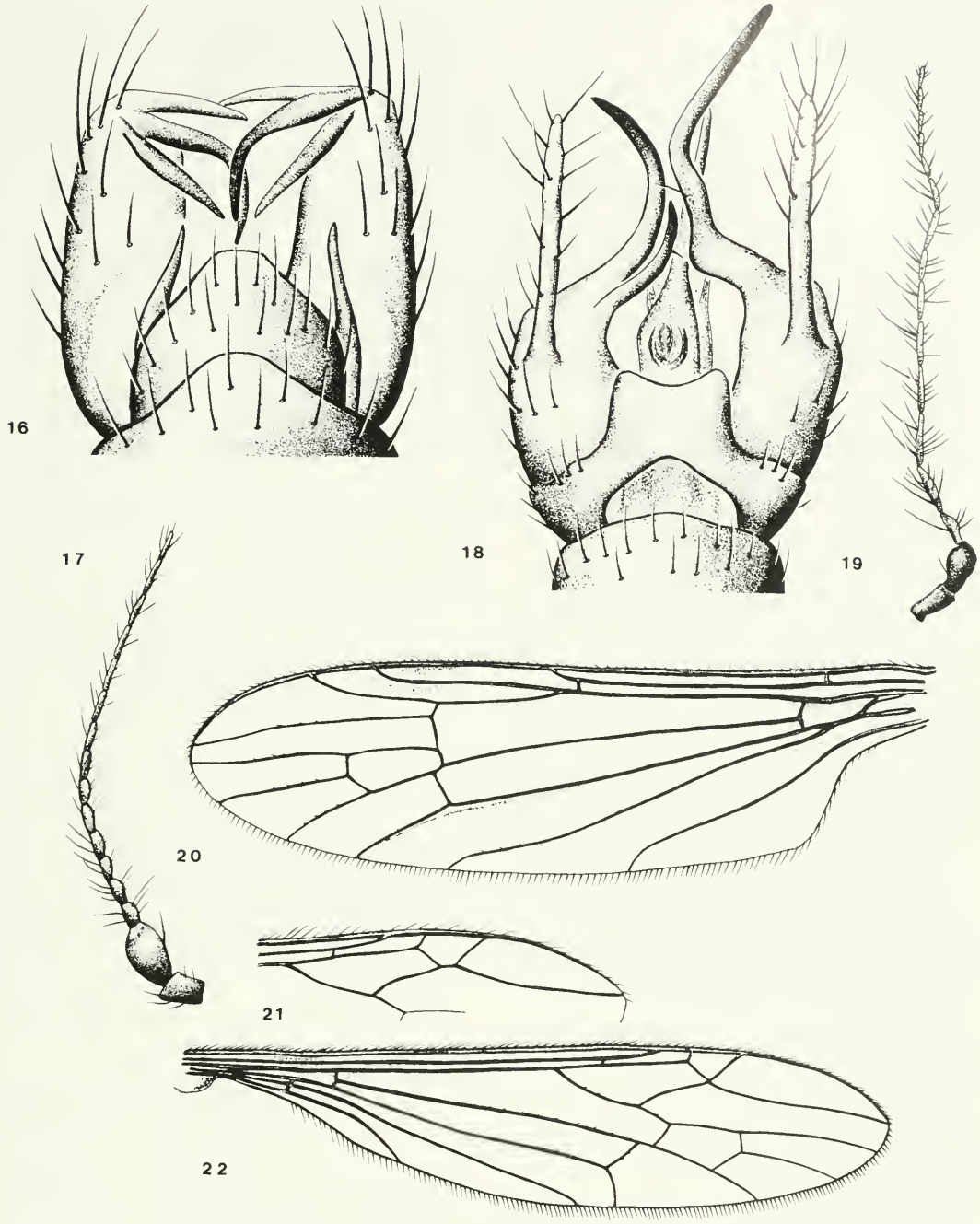
Diagnosis.—Size small for the subgenus. General body coloration yellowish brown; *Rs* beginning just before the end of Sc_1; *m-cu* located beyond fork of *M*; male genitalia, including hypopygium, asymmetrical.

Male.—Body length 3.0–4.2 mm. Head, rostrum, palpi and antenna brown. Antenna (Fig. 19) 16-segmented, 1.3 mm long; scape twice as long as wide; pedicel pyriform, about same length as scape; first flagellar segment about three-fourths length of pedicel, but narrower; all flagellar segments elongate with terminal segments nearly cylindrical; flagellum with verticils about as long as respective segments or slightly longer; apical segment nearly as long as proceeding segment.

Dorsal part of thorax brown, pleura reddish brown. Coxae, trochanters and rest of legs brownish. Wing clear, without darker marks except very light stigma; wing length 2.6–3.2 mm. Venation as usual for subgenus (Fig. 20): Sc_1 reaching slightly beyond origin of *Rs*, Sc_2 about its length before origin of *Rs*, *Rs* very slightly curved, about same length as R_3, *Rs* with only two branches; discal medial cell narrow, about 2.5 times as long as wide; cross-vein *m-cu* straight, more than 4.5 times as short as CuA_2; *m-cu* placed clearly beyond fork of *M*. Halter brownish yellow, 0.45 mm long.

Abdomen and genitalia brownish yellow, genitalia asymmetrical with darker tips; details shown in Fig. 18.

Female.—Similar to male, 4.1 mm long. Head, rostrum, palpi and antenna brown. Antenna scarcely reaching base of wing when bent backwards; yellowish brown; flagellar segments elongate, apical segments shorter, nearly oval; flagellum with



Figs. 16–22. 16–17, *Gnophomyia martyni*, holotype. 16, Male genitalia, dorsal view. 17, Antenna. 18–20, *Gonomyia* (*Paralipophleps*) *asymmetrica*. 18, Male genitalia, dorsal view, holotype. 19, Antenna, paratype. 20, Wing, paratype. 21–22, *Trentepohlia* (*Paramongoma*) *agri*. 21, Wing tip of female, paratype. 22, Wing of male, paratype.

verticils about length of respective segments or slightly longer.

Thorax brown. Coxae and trochanters brown, legs becoming yellow distally. Femur 1: 1.9, 2: 2.1, 3: 2.5 mm, tibia 1: 3.1, 2: 2.95, 3: 3.3 mm, tarsus 1: 2.65, 2: 2.55, 3: 2.5 mm. Wing length 3.3 mm. Haltere brownish yellow, 0.4 mm long.

Abdomen brown. Ovipositor brown dorsally, yellow ventrally, cerci and hypovalves brown.

Examined material.—Holotype ♂, number D-7-196, deposited in the Poinar collection.

Paratypes: ♂, number D-7-196A (genitalia damaged); ♀, number D-7-196B ♀, number D-7-196C, in the Poinar collection.

Discussion.—This new species differs from others in *Gonomyia* Meigen (1818) by its asymmetric male genitalia, which are very unusual in crane flies. Recent species of *Paralipophleps* Alexander, 1947, are characterized by a dark wing stigma, which is very light in the new species, but this could be due to preservation conditions in the resin. Only *G. pleuralis* (Williston 1896), belonging to same subgenus as the new species, occurs in the Lesser Antilles today (St. Vincent).

Gonomyia sp.

This species differs from *G. asymmetrica* by the very short vein Rs, but the male genitalia are completely damaged. The female is well preserved.

Examined material.—fragments, number D-7-201, and ♀, number D-7-201A, both in the Poinar collection.

Since the male genitalia are damaged, it is difficult to place this species in the subgenus *Lipophleps* Bergroth, (1915) or *Paralipophleps* Alexander, (1947) because the light wing stigma may have been modified by preservation.

Trentepohlia (Paramongoma) agri
Podenas and Poinar, new species
(Figs. 21–24)

Diagnosis.—The size is normal for members of this genus; male smaller than female. General body coloration brown, but some specimens are light or dark brown from changes occurring after entrapment in the resin; vein Sc_1 ends at one third length of R_{2+3}, Sc_2 ends opposite half length of *Rs*; male with elongate cylindrical gonocoxites; gonostyli elongated, flattened, with a spine on their frontal surfaces.

Male.—Body length 4.5–5.5 mm, wing length 3.7–4.8 mm. Head brown, rostrum, palpi and antenna greyish-brown. Antenna 15-segmented, yellowish, 1 mm long; scape three times as long as wide; pedicel oval, about half length of scape; first flagellar segment shorter than pedicel; all flagellar segments oval, apical segments elongated (Fig. 23); flagellum with verticils shorter than respective segments; apical segment as long as preceeding segment. Eyes approximate on top of head.

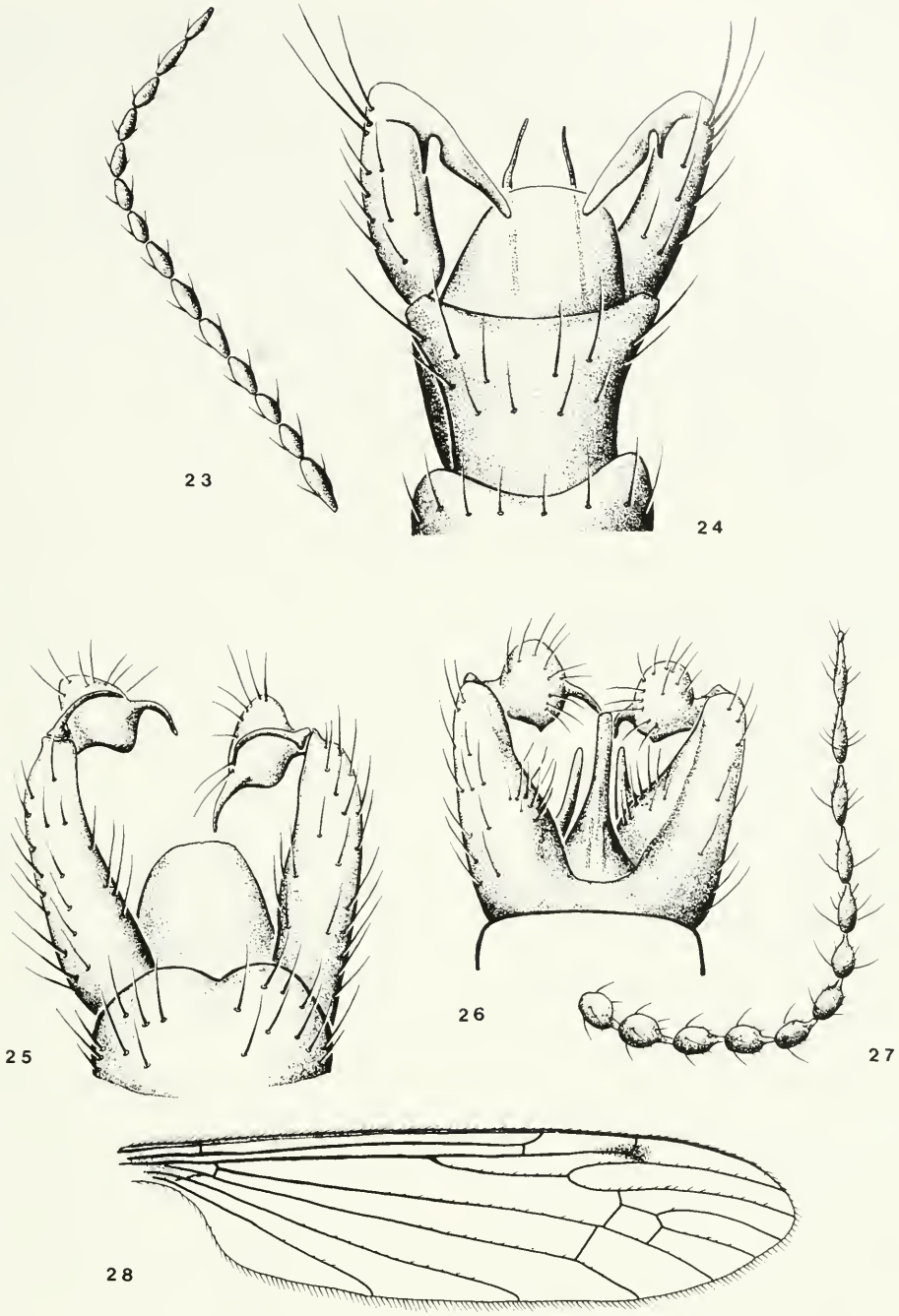
Dorsal part of thorax brown; prescutum with dark median stripe, pleura entirely brown. Coxae, trochanters and rest of legs brown. Femur 1: 6.1, 2: 5.6–6.0, 3: 5.5–6.6 mm, tibia 1: 7.2, 2: 6.4, 3: 6.0–6.7 mm, tarsus 2: 4.3, 3: 3.5–3.9 mm (tarsus 1 lacking in all specimens). Wing clear, without any darker marks. Venation as usual for genus (Fig. 22): *Sc* long, Sc_1 ending opposite one-third length of basal section of R_{2+3}, *Rs* slightly curved; discal medial cell twice as long as wide; cross-vein *m-cu* proximal to base of discal cell; tip of CuA_2 not reaching tip of A_1. Halter brown.

Abdomen and genitalia brown or greyish brown; genitalic details in Fig. 24.

Female.—Generally similar to male. Body length 8.2 mm, wing length 5.85 mm. Femur 1: 8.2, 2: 8.0, 3: 8.1 mm; tibia 1: 9.2, 2: 8.0, 3: 7.2 mm, tarsus 1: 7.1, 2: 6.2, 3: 6.2 mm. Venation differs from male by petiolate cell r_2 (Fig. 21)(variation of venation in this wing region is also known in extant species). Ovipositor protrudes beyond wing tips.

Examined material.—Holotype ♂, number D-7-208, deposited in the Poinar collection.

Paratypes: ♂, number D-7-208A; ♂,



Figs. 23–28. 23–24, *Trentepohlia* (*Paramongoma*) *agri*. 23, Flagellum of antenna, holotype. 24, Male genitalia, dorsal view, holotype. 25–28, *Dicranomyia* (*Dicranomyia*) *fera*. 25, 26, Male genitalia. 25, Dorsal view, paratype. 26, Ventral view, holotype. 27, Antennal flagellum, holotype. 28, Wing, paratype.

number D-7-208B (totally damaged genitalia); ♂ and ♂ fragments, number D-7-208C, ♀, number D-7-208D, (damaged wings), fragments, 2♂, numbers D-7-208E and D-7-208F, number D-7-208G and D-7-208H, all in the Poinar collection. El Valle area of Dominican Republic, Nr. ANSP 79760.

Discussion.—Four extant species belonging to the subgenus *Paramongoma* Brunetti, 1911, are known from the Antilles: *T. dominicana* Alexander, 1947; *T. manca* (Williston, 1896); *T. pallida* (Williston, 1896) and *T. niveitarsis* (Alexander, 1913). The new species, *T. (Paramongoma) agri,* is the commonest species of crane fly in Dominican amber.

LIMONIINAE

Dicranomyia (Dicranomyia) fera Podenas and Poinar, new species

(Figs. 25–28)

Diagnosis.—Size normal for genus. General body coloration brown. Wings longer than body. Wing with distinct elongate oval stigma; inner gonostylus small, approximately oval with beak-like spineless rostrum; antennal flagellum with short pedicel and verticils not exceeding the length of the respective segments.

Male.—Body length 4.25 mm. Head, rostrum, palpi and antennae brown. Antenna 14-segmented, reaching slightly beyond base of abdomen if bent backwards; scape elongate, about three times as long as thick; pedicel spherical; first flagellar segment (comparatively short) about same length as pedicel; proximal flagellomeres subglobular, remaining segments ranging from oval to elliptical, apical flagellomeres with short elongate tips (Fig. 27); flagellum with short verticils not longer than respective segments and with numerous stout setulae; apical flagellomere slightly longer than preceeding segment.

Thorax yellowish brown, prescutum with dark median stripe. Coxae, trochanters and rest of legs yellowish brown or dark brown (due to oxidization in resin). Femur 1: 3.3, 2: 4.4 mm, tibia 1: 4.5, 2: 4.2 mm, tarsus 1: 4.6 mm (fore leg preserved in specimen D-7-192 and midleg in specimen D-7-192A). Wing clear, with distinct, diffuse stigma, 4.4–5.3 mm long. Venation as usual for genus (Fig. 28): *Sc* relatively elongate, Sc_1 ending opposite $^4/_5$ length of *Rs*, Sc_2 about twice its length from tip of Sc_1, *Rs* very slightly curved, nearly 2.5 times basal deflection of R_{4+5}; discal medial cell relatively short; cross-vein *m-cu* straight, more than half as long as distal section of *Cu*, placed shortly before fork of *M*. Halter light brown.

Abdomen brown. Genitalia grayish brown, details in Figs. 25, 26: ninth tergite with shallow median emargination; gonocoxite long, outer gonostylus long and slightly curved; inner gonostylus small, oval shaped with beak-like, spineless rostrum; parameres with long and nearly straight apical appendage (as seen in ventral view of genitalia of specimen No D-7-192); aedeagus long and narrow.

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-192, deposited in the Poinar collection.

Paratype ♂, number D-7-192A, deposited in the Poinar collection.

Discussion.—Both this species and the following one are unique in the genus by lacking rostral spines on the inner gonostylus. Recent species of *Dicranomyia* Stephens, 1829, distributed in adjacent islands are: *D. borinquenia* (Alexander 1968); *D. brevivena torrida* (Alexander 1932); *D. calliergon calliergon* (Alexander 1939); *D. calliergon polygrapha* (Alexander 1939); *D. distans* Osten Sacken, 1859; *D. divisa* (Alexander 1929); *D. farri* (Alexander, 1964); *D. indefensa* (Alexander, 1939); *D. lewisi* (Alexander 1964); *D. reticulata* (Alexander 1912); *D. torulosa* (Alexander 1968) and *D. trinitatis* (Alexander 1931). Both new species clearly differ from all other described species by the male genitalia, especially the naked rostrum of the

inner gonostylus. Alexander described *Dicranomyia* as a subgenus of *Limonia* Meigen, 1803, but according to current thought *Dicranomyia* is a distinct, large and widely distributed genus (Savchenko et al. 1992).

Dicranomyia (Dicranomyia) lema Podenas and Poinar, new species

(Figs. 29–32)

Diagnosis.—Size normal for genus. General body coloration brown. Wings longer than body. Ninth tergite with broad emargination; outer gonostylus long and slightly curved; inner gonostylus with enlarged oval shape with long spineless rostrum; can be separated from the previous species by the relatively short *Sc* vein with Sc_1 ending near one-third the length of *Rs* and Sc_2 about the same length as Sc_1 (in *D. fera, Sc* is relatively long and Sc_1 ends opposite 4/5th the length of *Rs*).

Male.—Body length 4.2–7.0 mm. Head and rostrum brown, palpi and antenna dark brown proximally, lighter distally. Antenna 14-segmented, 0.8–1.3 mm long, reaching wing base if bent backwards; scape elongate; pedicel spherical; first flagellar segment about same length as pedicel; proximal flagellar segments oval, apical segments elongate and nearly cylindrical (Figs. 30, 31); individual segments with short pedicels in specimen from ANSP collection, not seen in other specimens; flagellum with short verticils, usually not longer than respective segments; apical segment large, nearly as long as preceding segment.

Dorsal part of thorax brown; pleura yellowish brown with darker spots. Coxae, trochanters and rest of legs brown. Femur 1: 3.1–5.5, 2: 3.7–6.3, 3: 6.5 mm, tibia 1: 3.8–6.3, 2: 6.9, 3: 7.0 mm; tarsus 3: 6.5 mm (tarsus 1 and 2 missing in both specimens). Wing clear, brownish, with slightly darker marks along veins, without stigma, 4.6–7.1 mm long. Venation as usual for genus (Fig. 32): *Sc* relatively short, Sc_1 ending near one-third length of *Rs*, Sc_2 about same length as Sc_1, *Rs* very slightly curved, nearly straight, almost three times basal deflection of R_{4+5}; R_2 at tip of R_1; discal medial cell relatively short; crossvein *m-cu* straight, slightly longer than distal section of CuA_2, placed shortly beyond fork of *M*. Haltere brownish.

Abdomen and genitalia yellowish brown with distal margins of tergites and sternites darker; details evident in Fig. 29: ninth tergite with broad emargination; outer gonostylus long and slightly curved; inner gonostylus oval with long spineless rostrum; paramere with long and nearly straight apical appendage; aedeagus long and narrow.

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-193, deposited in the Poinar collection.

Paratypes: ♂, number D-7-194 deposited in the Poinar collection; ♂, El Valle area of Dominican Republic, Nr. ANSP 79761 (abdomen of this specimen, especially distally, is swollen from air bubbles).

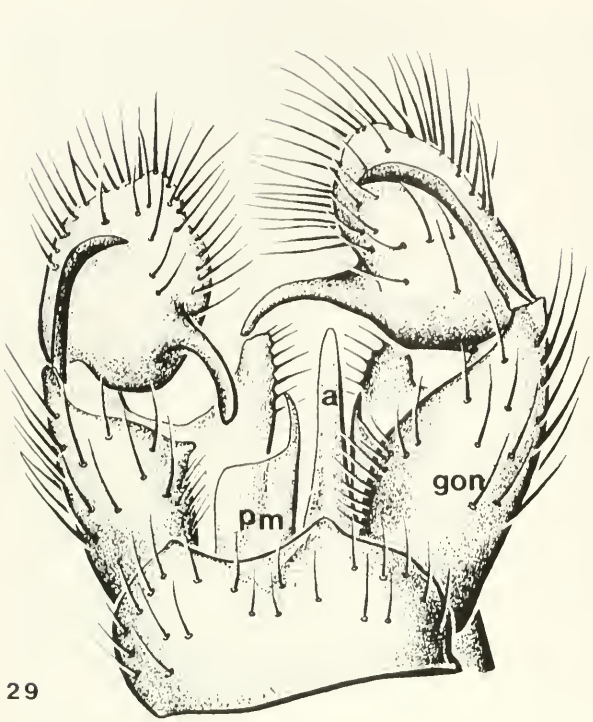
Rhipidia (Rhipidia) mira Podenas and Poinar, new species

(Figs. 33–36)

Diagnosis.—Size normal for genus. General body coloration brown to yellowish brown. Proximal flagellomeres bipectinate, with outer segments elongate cylindrical. Ninth tergite with nearly straight distal margin; gonocoxite elongated with ventro-mesal projection; outer gonostylus long and slightly curved at apex. Wing pattern with six dark spots in costal region and weaker spots on wing apex and cross-veins.

Male.—Body length about 5.3 mm, wing length 5.1 mm. Head dark brown, rostrum and palpi (Fig. 35) brown. Antenna brown proximally, brownish yellow distally, 14-segmented, reaching wing bases if bent backwards; scape elongate, about twice as long as thick; pedicel ovoid; first flagellar segment comparatively short, about same length as scape; proximal flagellomeres bipectinate, outer segments elongate cyclindrical (Fig. 34); flagellar verticils as long as respective segments.

Thorax dorsally and laterally brown.



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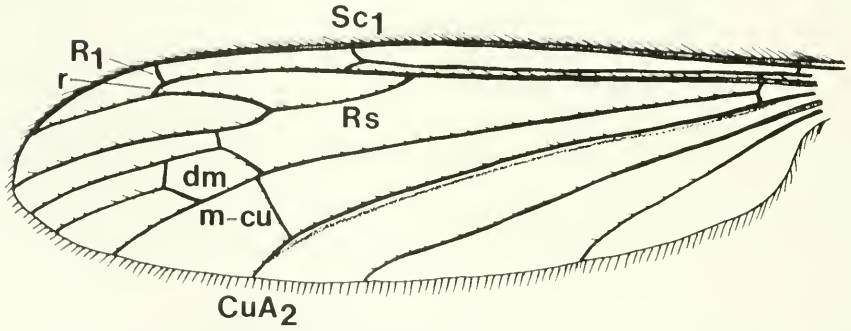

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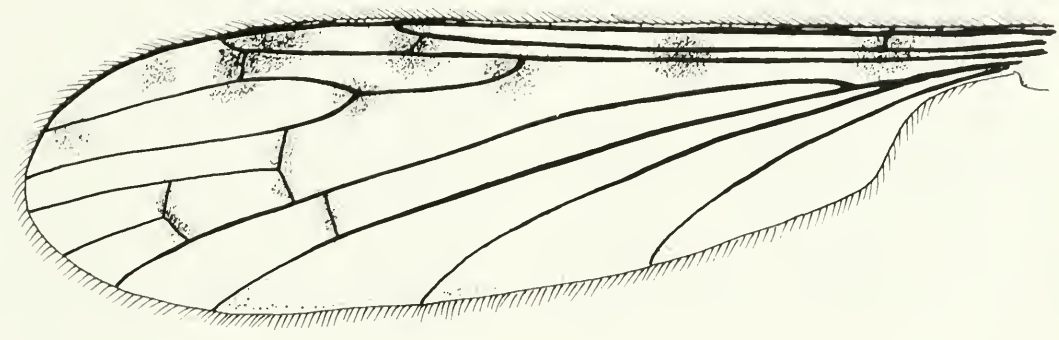
Figs. 29–32. *Dicranomyia* (*Dicranomyia*) *lema*. 29, Male genitalia, dorsal view, holotype. 30, Flagellum of antenna, holotype. 31, Flagellum of antenna, paratype. 32, Wing, holotype. (See Materials and Methods for abbreviations.)

Coxae dark brown, rest of legs yellowish brown with darker tips on femora. Femur 1: 3.55 mm, tibia 1: 4.4 mm (other legs near body, but not clear which is mid or hind). Wing with distinct oval spots along costal margin and darkening along crossveins (Fig. 36), 5.1 mm long. Venation usual for genus: *Sc* relatively elongate, Sc_1 ending opposite $^4/_5$ length of *Rs*, Sc_2 about its length from tip of Sc_1, *Rs* very slightly curved, nearly twice as long as basal deflection of R_{4+5}; R_2 near tip of R_1; discal medial cell



Figs. 33–36. *Rhipidia (Rhipidia) mira,* holotype. 33, Male genitalia, dorsal view. 34, Flagellum of antenna. 35, Maxillary palpus. 36, Wing.

about twice as long as wide; crossvein *m-cu* straight, nearly 3.3 times shorter than distal section of CuA_2, placed clearly before fork of *M.* Halter brownish yellow.

Abdomen yellowish brown with caudal margins of tergites darkened. Genitalia yellowish brown; details evident in Fig. 33: ninth tergite with nearly straight distal margin; gonocoxite elongated with ventro-mesal projection; outer gonostylus long and curved at apex; inner gonostylus large, oval with two long rostral spines; paramere wide basally and sharp distally with long and nearly straight apical appendage; dorsal protuberance on inner gonostylus near base of rostrum; aedeagus long and narrow.

Female.—Unknown.

Examined material.—Holotype ♂, number D-7-200, deposited in the Poinar collection.

Discussion.—Extant species of *Rhipidia* Meigen, 1818 distributed in adjacent islands are: *Rh. bellingeri* (Alexander 1964); *Rh. bipectinata* Williston 1896; *Rh. calverti* Alexander 1912; *Rh. domestica domestica* Osten Sacken 1859; *Rh. pratti* (Alexander 1950); *Rh. schwarzi* Alexander 1912; *Rh. subcostalis* Alexander 1922; *Rh. subpectinata subpectinata* Williston 1896; *Rh. tetraleuca* (Alexander 1937); *Rh. unipectinata* Williston 1896 and *Rh. willistoniana* (Alexander 1929). Alexander described *Rhipidia* as a subgenus of *Limonia* Meigen 1803, but some consider *Rhipidia* as a separate, large and widely distributed genus (Savchenko et al. 1992). These and other recent, undescribed *Rhipidia* species, which the senior author examined from the Antilles, usually have simple antennae, not as in the present fossil. *Rhipidia mira* differs from all recent species not only by the male genitalia, but also by the shape of the palpi. The wing pattern is more similar to that of North American species.

Acknowledgments

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THE IDENTITY OF TWO UNPLACED NEW WORLD MEGASTIGMINAE (HYMENOPTERA: TORYMIDAE)

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Abstract.—Two previously unplaced taxa of Torymidae are recognized. *Megastigmus mendocinus* Kieffer and Jörgensen 1910 is transferred to the genus *Torymoides* (Torymidae), **new combination,** and is placed as a **new junior subjective synonym** of *Torymoides sulcius* (Walker), one of the most widespread torymid parasitoids of Cecidomyiidae in the New World. *Megastigmus flavipes* Ashmead 1886 is transferred to the genus *Gastrancistrus* (Pteromalidae), **new combination,** and *Gastrancistrus biguttatus* (Girault) 1917 is placed as a **new junior subjective synonym** of *Gastrancistrus flavipes* (Ashmead).

Key Words: *Megastigmus mendocinus, Torymoides mendocinus, Megastigmus flavipes, Gastrancistrus flavipes,* new synonymy

In the course of preparing a world catalog for the subfamily Megastigminae the senior author discovered two species of *Megastigmus* that have eluded positive recognition since their description. *Megastigmus mendocinus* Kieffer and Jörgensen (1910) is the only species (of 168) reported from South America; its type material has never been located. *Megastigmus flavipes* Ashmead (1886) is known only from the holotype, which was fragmented sometime after its description, and all that now remains is a single forewing, a hindleg, and the tibia from another leg. The purpose of this paper is to confirm the identity and correct nomenclature for these two taxa, the latter of which is transferred to the family Pteromalidae.

Torymidae

Torymoides sulcius (Walker)

Callimome sulcius Walker 1839: 64. Holotype female BMNH, examined.

Callimome caburus Walker 1839: 63–64. Holotype male BMNH, examined.

Megastigma cecidomyiae Ashmead 1887: 185–186. Lectotype female USNM, examined.

Lochites auriceps Ashmead 1894: 153. 2 syntype females USNM, examined.

Torymus ventralis Howard 1897: 135. 2 syntype males BMNH (1 syntype), USNM (1 syntype), both examined.

Torymus howardii Dalla Torre 1898: 307. Objective replacement name for *Torymus ventralis* Howard 1897: 135 *nec* Fonscolombe 1832: 286.

Megastigmus fulvus Cameron 1904: 58. Holotype female BMNH, examined.

Megastigmus mendocinus Kieffer and Jörgensen 1910: 410. Female syntypes lost. **New Synonymy.**

Megastigmus mendocinus Kieffer and Jörgensen is the only species of the genus reported from South America. It was col-

lected in Cordillera de Mendoza, Provincia Mendoza, Argentina. No one has been able to locate the type material of Kieffer and Jörgensen (De Santis, personal communication, Gagné 1994) so that judgment about most of their species must be based on original descriptions and an examination of host information, both of which are remarkably good (Grissell 1995). The species was described based on specimens reared from a cecidomyiid gall, *Oligotrophus lyciicola* Kieffer and Jörgensen. Only four of 168 species of Megastigminae are positively associated with Diptera, and of these, only two are known as parasitoids of Cecidomyiidae (Grissell, in press). Therefore the host association alone casts some suspicion on the placement of *mendocinus* in *Megastigmus.*

Within the subfamily Megastigminae, the only species known from South America is *mendocinus.* In the New World *Megastigmus albifrons* Walker is known to occur as far south as Guatemala, all other species being confined to the Nearctic Region. Thus, distribution of known species also argues against the current generic placement.

Kieffer and Jörgensen described the female of *mendocinus* as 1.8 mm in length, which is exceptionally small for species of *Megastigmus.* The body was described as yellow-red, with parts of the thorax metallic green and the dorsum of the abdomen brownish. The stigma was described as being circular. This description readily fits the torymid *Torymoides sulcius* (Walker 1839), which also happens to be the most commonly collected, widespread Neotropical torymid parasitoid associated with cecidomyiids. It might be assumed, based on the otherwise comprehensive and lengthy paper of Kieffer and Jörgensen, that they would, by chance, have described the most common species. In this case we believe they called it *M. mendocinus.* One synonym of *Torymoides sulcius* is *Megastigmus cecidomyiae* Ashmead (1887), a further indication that some species in the two genera might be confused based on the somewhat enlarged stigma of the forewing in *T. sulcius.*

For the above reasons, we place *Megastigmus mendocinus* Kieffer and Jörgensen as a junior subjective synonym of *Torymoides sulcius* (Walker). The remaining synonyms listed above were explained in Grissell (1995).

The known distribution of this species now encompasses Florida and Texas (Peck 1951) south to Mexico, Grenada, St. Vincent, St. Kitts, Montserrat, Nicaragua, Peru, Argentina, and Brazil (De Santis 1978, 1979).

Pteromalidae

Gastrancistrus flavipes (Ashmead), **new combination**

Megastigmus flavipes Ashmead 1886: 128 (*nec* Ashmead 1888). Holotype male, Florida USNM, examined.

Miscogaster biguttata Girault 1917: 97. 4 male syntypes, [Florida] USNM, examined. **New synonymy.**

Megastigmus flavipes was discussed by Milliron (1949) who placed it as an unrecognized species in his revision of Nearctic species. Even in 1949 all that remained of the single known specimen (the holotype) was a wing and hind leg. Milliron (1949) commented that, based on the original description, the species might not be a *Megastigmus,* but based on the distinctive stigmal vein it might be a megastigmine torymid.

The stigmal vein of *M. flavipes* is enlarged and distinctive enough so that when initially examined by the senior author, it was apparent that the species might be placed in the pteromalid genus *Gastrancistrus.* The junior author has been working on a revision of that genus, and based on the type locality (Jacksonville, Florida) and enlarged stigma, the fragmentary wing and leg was readily associated with a series of specimens of *Gastrancistrus* described from that same locality by Girault (1917). The pale tibia and the restriction of the darker coloration on the wing to the stigmal

vein and its immediate vicinity is the same as that found in *Miscogaster biguttata* Girault, which was transferred to *Gastrancistrus* by Heydon and Bouček (1992: 476). *Gastrancistrus biguttatus* (Girault) is the earlier name and is here placed as a junior subjective synonym of *flavipes* (Ashmead) which is transferred from *Megastigmus* as a new combination in the genus *Gastrancistrus.*

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DESCRIPTION OF THE PUPA OF *AEDES CRETINUS* EDWARDS, A KEY TO THE PUPAE OF THE *ALBOPICTUS* SUBGROUP, SUBGENUS *STEGOMYIA* THEOBALD, GENUS *AEDES* MEIGEN, AND CHARACTERS TO SEPARATE THE EUROPEAN *STEGOMYIA* SPECIES (DIPTERA: CULICIDAE)

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Abstract.—The description of the unknown pupa of *Aedes cretinus* and a key to the known pupae of the *albopictus* subgroup, *scutellaris* group, subgenus *Stegomyia,* genus *Aedes* are presented. The three species of subgenus *Stegomyia,* genus *Aedes,* which occur in Europe, are characterized.

Key Words: Aedes cretinus, pupa, *albopictus* subgroup, European *Stegomyia*

Aedes (*Stegomyia*) *cretinus* Edwards, 1921, is the only species of subgenus *Stegomyia* indigenous to Europe. It belongs to Group C of Edwards (1932), the *scutellaris* group. It has been reported from Greece, Georgia (Mattingly 1953), Turkey and Cyprus (Lane 1982). Knight and Hurlbut (1949) divided the group into the *scutellaris, albopictus* and *mediopunctatus* subgroups and placed *Ae. cretinus* in the *albopictus* subgroup along with nine other species. Mattingly (1952, 1965) transferred *Ae. granti* (Theobald) to *scutellaris* subgroup and *Ae. galloisi* Yamada to Edwards Group B which Huang (1972b) reassigned to the *albopictus* subgroup. Moreover, *Aedes* (*Stegomyia*) *patriciae* Mattingly, 1954, *Aedes* (*Stegomyia*) *seatoi* Huang, 1969, *Aedes* (*Stegomyia*) *sibiricus* Danilov and Filippova (1978) and *Aedes* (*Stegomyia*) *galloisioides* Liu and Lu (1984) have been added to the *albopictus* subgroup (Huang 1972a, 1979).

The pupae of all species of the *albopictus* subgroup have been described (Huang 1972a, Edwards 1941) except *Ae. sibiricus* and *Ae. galloisioides* and *Ae cretinus,* which is characterized below. A key for the identification of known pupae of the subgroup follows. The adult female, male and larva of *Ae. cretinus* were described by Mattingly (1954).

Aedes (*Stegomyia*) *albopictus* (Skuse) was first reported in Europe by Adhami and Murati (1987) in Albania, then in Italy in 1990 (Sabatini et al. 1990). It has continued to spread in Europe (Romi 1995) but as yet has not been found in Greece. However, *Ae. cretinus* in Greece has been misidentified as *Ae. albopictus,* causing undue anxiety, fearing a potential for a dengue fever outbreak (A. Samanidou, personal communication, 1997). Indeed the two species are quite similar (Lane 1982) and knowing all of their life stages, including the pupa, will be of benefit.

Three species of subgenus *Stegomyia* presently occur in Europe, *Ae. aegypti* (Linnaeus) (Christophers 1960), *Ae. albopictus* and *Ae. cretinus* (Mattingly 1953). Characters to distinguish the adult females, pupae and larvae are given in Table 2.

MATERIALS AND METHODS

Methods of collecting mosquitoes in the field followed those given by Belkin et al.

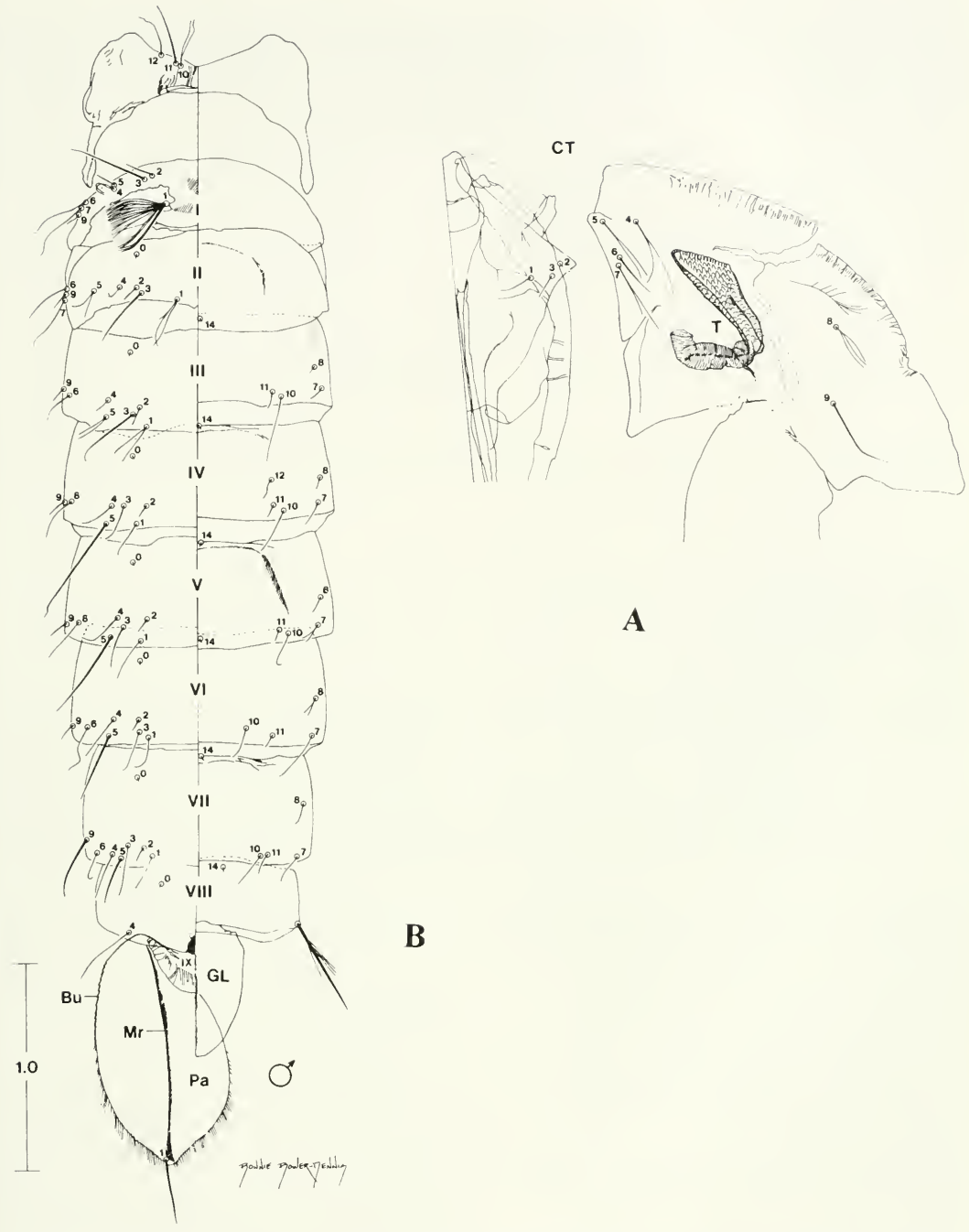

Fig. 1. Pupa of *Aedes cretinus*. A, Cephalothorax. B, Metathorax and abdomen; dorsal-left, ventral-right. Bu = external buttress; CT = cephalothorax; GL = genital lobe; Mr = midrib of paddle; Pa = paddle; T = respiratory trumpet.

Table 1. Pupal chaetotaxy of *Aedes cretinus*.

Seta	Cephalothorax	Abdominal Segments							
		I	II	III	IV	V	VI	VII	VIII
0	—	—	1	1	1	1	1	1	1
1	1	9–13 (11)	2–3 (3)	1–2 (2)	1–2 (1)	1	1	1	—
2	1	1	1	1	1	1	1	1	—
3	1	1	1	1	1–2 (2)	1	1	1	—
4	1–2 (1)[1]	2–4 (2)	1–4 (1)	1–4 (2)	1–2 (1)	1–2 (2)	1	1	1
5	1–2 (2)	1–2 (1)	1–3 (2)	1–2 (2)	1	1	1	1	—
6	1	1	1	1	1	1	1–2 (1)	1	—
7	1–2 (2)	1	1–2 (1)	1–4 (1)	1–2 (1)	1–5 (?)	1	1	—
8	1–3 (2)	—	—	1–2 (1)	1	1–2 (1)	2–3 (2)	1–3 (1)	—
9	1	1	1	—	1	1	1	1–2 (1)	1–2 (1)
10	1–3 (2)	—	—	1	1–2 (1)	1	1	1	—
11	1	—	—	1	1	1	1	1	—
12	1–2 (2)	—	—	—	—	1	—	—	—
14	—	—	—	1	1	1	1	1	1

[1] Range followed in parenthesis by the mode.

(1965) and preparing the specimens for study follow the procedures of Wood et al. (1979). A female of *Aedes cretinus* was collected in Athens, Greece, by A. Samanidou, blood fed and held in a 9-dram vial until it oviposited. Eggs were seasoned then hatched and larvae mass reared to the fourth instar, then several were reared individually. The larval and pupal exuviae were preserved and subsequently slide mounted in Canada balsam. Similarly, fourth instar larvae from a colony of *Ae. cretinus* at Notre Dame University, started from specimens collected on the island of Crete, were reared individually and made available for this study by C. Taafe.

The *Aedes albopictus* pupae were from two sources: Nepal-reared from larvae collected in bamboo stumps in Ranibas, Sinduli Garhi District, 1991 (4 ♀ and 6 ♂), and U.S.A.—individual rearings of larvae collected in Vero Beach, Florida, 1997 (9 ♀ and 1 ♂).

The *Ae. aegypti* pupae (8 ♀ and 14 ♂) were obtained from a colony at the Naval Medical Research Center, Bethesda, Maryland, provided by H. S. Hurlbut, 1947.

Abbreviations used in the description are: Le Pe = larval exuviae and pupal exuviae, and br = branches.

Description

Aedes (*Stegomyia*) *cretinus* Edwards (Fig. 1)

Pupa.—Position and size of setae as in Fig. 1; range and modal number of branches in Table 1. *Cephalothorax:* Seta 7-CT 1.29–2.2 length of 6-CT, both single; trumpet medium to dark brown, reticulate, length 0.46–0.65 mm, pinna 0.07–0.20 mm, index 1.46–1.73. *Abdomen:* light to medium brown, darker sublaterally; seta 1–II with 2–3 br from base; 6-VI single, rarely double, 0.7 length of 9-VII; 9-II not much smaller than 9-III–V; 9-V 0.8 length of 9-VI; 9-VI 0.3 length of 9-VII, subequal in size; 9-VII single, smooth, stouter than 5-VI; 9-VIII stout, single, rarely with 2 main stems, with several long aciculae near middle, about 0.2 length of seta. *Paddle:* Outer and inner margins fringed in apical 0.6, fringe length 0.05 mm, midrib extending to near apex, seta 1-P rather stout, single, 0.29–0.4 length of paddle.

Specimens examined.—The description was based on the following: Greece, Attiki District, Athens, Kifissa, IX-30-97, 2 ♀ Le, Pe, 4 ♂ Le, Pe; Crete, VII-93, 5 ♀, Le, Pe, and 7 ♂, Le, Pe. (L.E. Munstermann) (from

Table 2. Distinguishing characters of three *Stegomyia* species in Europe.

Character	*aegypti*	*albopictus*	*cretinus*
		ADULT FEMALE	
Scutum	Lyre-shaped pale marking	Narrow pale stripe, no sub-median stripes	Narrow pale stripe, with sub-median stripes
Abdominal sterna III–V	Pale-scaled	Dark-scaled, basal pale bands	Dark-scaled, basal pale bands
Clypeus	With scales	No scales	No scales
Mesepimeron	2 scale patches	Single V-shaped scale patch	Single V-shaped scale patch
Fore- and mid-tarsomeres	Toothed	Simple	Toothed
		PUPA	
Seta 7-CT/ seta 6-CT	7-CT 0.53–0.77 length of 6-CT	7-CT 1.25–2.7 length of 6-CT	7-CT 1.29–2.2 length of 6-CT
Seta 1-II	2–4 br	4–8 br	2–3 br
Seta 9-VIII	3–8 br	1–2 br	1–2 br
Seta 9-VIII length	NA	Reaching beyond paddle fringe	Not reaching to paddle fringe
Paddle index	1.06–1.31	1.22–1.38	1.4–1.7
Paddle fringe	Absent	Present	Present
		FOURTH INSTAR LARVA	
Seta 4-X, No. Pairs on grid	5 pairs	4 pairs	4 pairs
Branching of seta 4-X	Setae branched	Setae single	Mostly single some double
Comb scale	Prominent apical and sub-apical spines	Prominent apical spine, tiny basal spinules	Prominent apical spine, tiny basal spinules
Setal support plates—setae 9-I2-M, T	Prominent spine	Short thin spine	Small spine
Seta 7-C	Single	Double	2–3 br
Siphon index	2.5 or less	2.0 or less	2.4 or more

University of Notre Dame colony, C. Taafe).

Key to The Known Pupae of the *Albopictus* Subgroup, *Scutellaris* Group, Subgenus *Stegomyia*

In order to identify the pupa of *Ae. cretinus*, it is placed in the following key to the known pupae of the *albopictus* subgroup. The *Aedes unilineatus* (Theobald) pupa was incompletely described by Edwards (1941), therefore its placement in the key is tentative. The key was adapted from Huang (1972a).

1. Seta 9-III–V strongly developed, thickened, much stouter than 9-II ..... *seatoi* Huang
– Seta 9-III–V not strongly developed, about same magnitude as 9-II 2

2(1). Seta 9-VI much stouter than 9-V, at least twice as long 3
– Seta 9-VI about as thick as 9-V, less than twice as long 4

3(2) Seta 9-VI usually single, aciculate; seta 9-VIII reaching beyond paddle fringe, ... *downsi* Bohart and Ingram
– Seta 9-VI single, smooth; seta 9-VIII not reaching beyond paddle fringe .... *subalbopictus* Barraud

4(2). Seta 9-VII usually single, stout, aciculate or split at tip 5
– Seta 9-VII usually single, smooth 7

5(4). Paddle margins with rather short fringe; seta 9-VIII single, strong, aciculate, just reaching paddle fringe ..... *novalbopictus* Barraud
– Paddle margin with long fringe; seta 9-VIII with 2 main stems (1–2), each aciculate, reaching beyond paddle fringe 6

6(5). Seta I–II with 8 or more branches; seta 1-P 0.5 length of paddle .... *flavopictus* Yamada

– Seta 1–II usually with fewer than 8 branches; seta 1-P 0.3 length of paddle .... *unilineatus* (Theobald)

7(4). Seta 9-VIII not reaching beyond fringe of paddle 8

– Seta 9-VIII reaching beyond fringe of paddle 9

8(7). Seta 1–II with 5–7 branches; seta 9-VIII usually double ..... *patriciae* Mattingly

– Seta 1–II double or triple; seta 9-VIII usually single ..... *cretinus* Edwards

9(7). Seta 9-VIII with 2 branches; seta 10-CT about 0.6 length of seta 11-CT; seta 2-VII medial to seta 1-VII *pseudalbopictus* (Borel)

– Seta 9-VIII usually single; seta 10-CT subequal to seta 11-CT; seta 2-VII laterad of seta 1-VII ..... *albopictus* (Skuse)

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REDESCRIPTION OF *RAPITES* VILLIERS 1948 (HETEROPTERA: REDUVIIDAE: PEIRATINAE)

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Abstract.—*Rapites,* an exclusively Afrotropical genus, and its only species, *R. elongatus* Villiers (= *R. villiersi* Schouteden, **new synonymy**) are redescribed. Measurements and ratios are included.

Key Words: Heteroptera, *Rapites, Rapites elongatus,* Reduviidae

The present revision was carried out in order to redescribe the genus *Rapites* Villiers and its only included species. Previously unused characters are presented, and *R. villiersi* Schouteden is synonymized with *R. elongatus* Villiers based on comparison of the two holotypes.

MATERIAL AND METHODS

The terminology used for external morphology follows Coscarón (1983), Lent and Jurberg (1966), and Lent and Wygodzinsky (1979). The measurements and ratios follow Coscarón (1989). For this revision, a total of four measurements and 11 ratios were selected. Extraction, dissection, inflation, and drawings of the male genitalia were performed according to Coscarón (1983). The terminology employed for the characters of the female genitalia was detailed in Coscarón (1994a).

SYSTEMATICS

Rapites Villiers

Rapites Villiers 1948: 230; Maldonado-Capriles 1990: 368. Type species: *Rapites elongatum* Villiers 1948, by original designation.

Redescription.—Head dark brown; without pilosity around antenna and between eyes. Postocular region rounded. In lateral view, eyes surpassing neither superior nor inferior edges of head, occupying more than half length of head. Ocelli not on a tubercle. Neck 1 + 1 tubercles developed. Lateral margin of pronotum carinated along its entire length. Anterior lobe with reduced pilosity and hairs and no granulations. Sulci on anteror lobe of pronotum not distinct, with pilosity and reduced hairs. Scutellum with reduced hairs, pilosity, and granulations, and without rugosities. Suture of metapleuron curved. Posterior process of scutellum acuminate. Fore and mid tibiae distally swollen (Fig. 1), spongy fossa not preceded by a small prominence. Femora without low setigerous tubercles on lower surface. Only macropterous form known.

Rapites elongatus Villiers

(Figs. 1, 2)

Rapites elongatum Villiers 1948: 230; Maldonado-Capriles 1990: 368; Kerzhner 1992: 52.

Rapites villiersi Schouteden 1952: 325; Maldonado-Capriles 1990: 368. **New synonymy.**

Male.—General aspect as in Fig. 1. Head (Fig. 2a) dark brown with whitish pilosity, not granulated. Antenna uniformly colored,

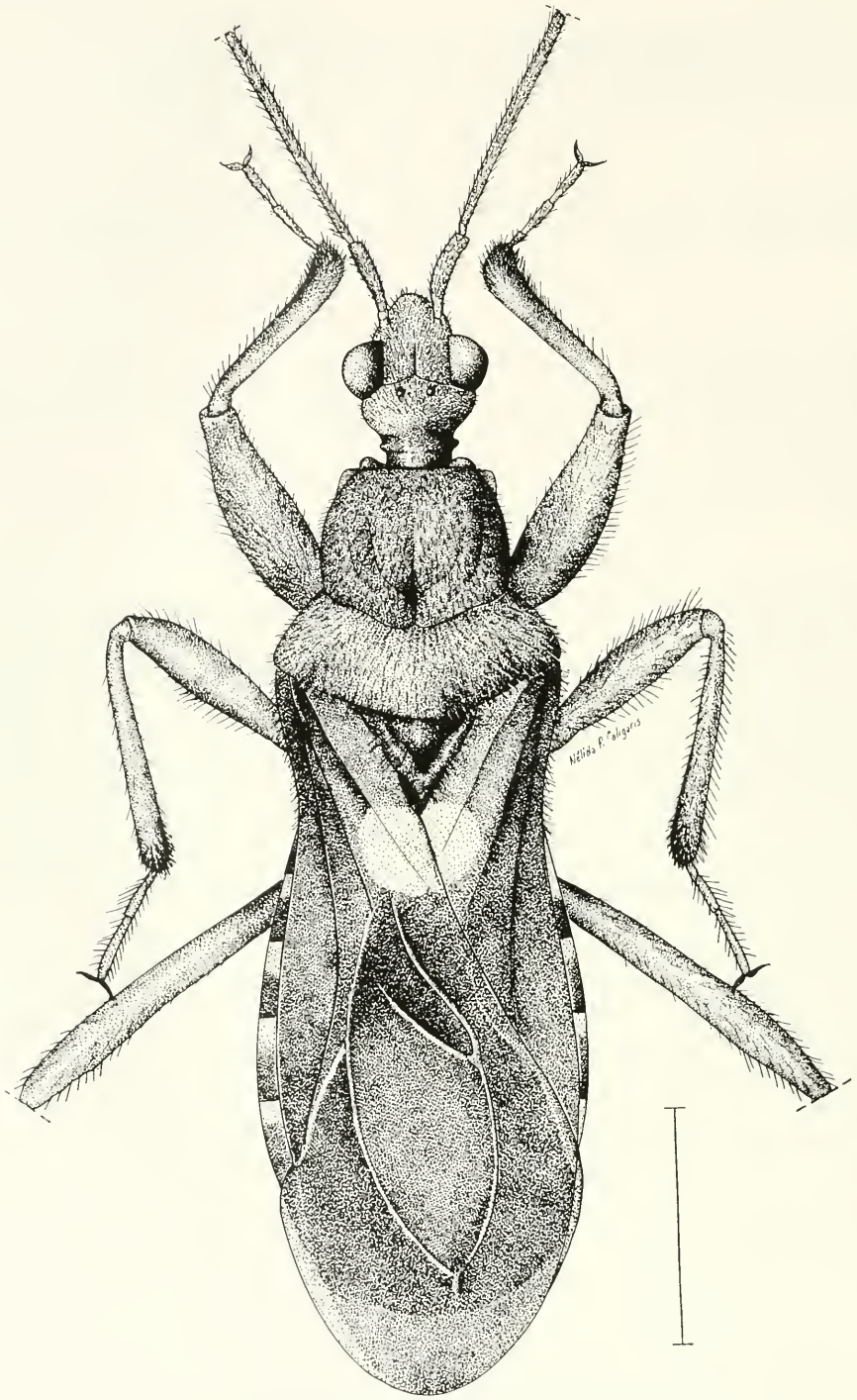

Fig. 1. *Rapites elongatus*, general aspect of the male. Scale line = 2.0 mm.

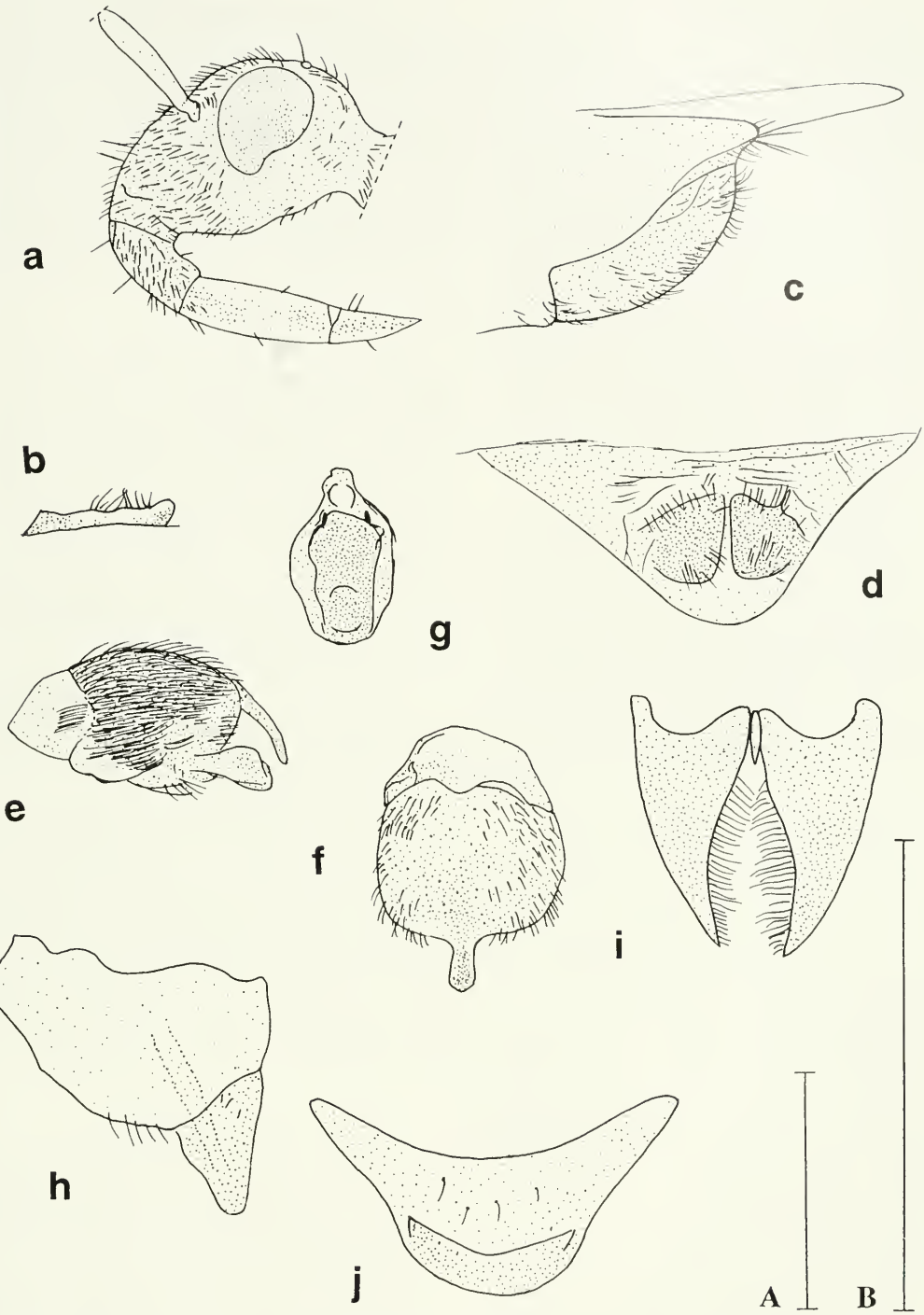

Fig. 2. *Rapites elongatus*. a, Head, lateral view. b, Scutellum, lateral view. c, Male genitalia, lateral view. d, Male genitalia, posterior view. e, Pygophore and parameres, lateral view. f, Pygophore, ventral view. g, Aedeagus. h, Gonocoxite and gonapophysis VIII. i, gonocoxite IX. j, Tergites IX and X. Scale line = 2.0 mm; line A for a–d and line B for e–j.

dark brown. Pronotum anterior lobe (Fig. 1) dark brown except sulci with pale brown pilosity, light brown hairs over surface and edges, and not granulated. Sulci without granulations. Depression between pronotal lobes distinct. Posterior lobe (Fig. 1) dark brown, with light brown pilosity and hairs, without granulations. Scutellum (Fig. 2b) dark and light brown (not uniformly pigmented) and with light brown hairs; principal body edges of scutellum rounded.

Hemelytra (Figs. 1, 2c) passing apex of abdomen. Predominating color dark brown, except a yellowish dot apically on clavus and adjacent part of corium. Light brown hairs in corium.

Legs dark brown.

Conexivum dorsally visible. Pattern of conexivum as in Fig. 1. Urosternites light and dark brown (not homogeneously pigmented) and with whitish pilosity. Last segments of abdomen ventrally dark brown.

Genitalia (Figs. 2c–g) with medial distal region of medial process of pygophore straight and extremely acute (Figs. 2e, f). Parameres subtriangular (Fig. 2d) with pilosity and setae in external and internal views. Basal plate simple (Fig. 2g).

Female.—Hemelytra not passing apex of abdomen. Genitalia (Figs. 2h–j) with gonocoxites VIII and gonopophysis, gonocoxite IX, and IX and X tergites as in Figs. 2h, i, j, respectively. IX and X tergites (Fig. 2j) intersegmental line not entire.

Measurements and ratios.—Total length: male: 9.51, female: 7.29; width pronotum: male: 2.22, female: 2.36; width abdomen: male: 3.05, female: 2.63; head length/head height: male: 1.16, female: 1.11; length anteocular region/length postocular region: male: 1.26, female: 1.00; eye length/eye width: male: 1.72, female: 1.30; eye height/head height: male: 0.62, female: 0.59; length eye interocular region/ocellar diameter: male: 1.36, female: 1.35; antennal segments length relationships: antennal segment 1/antennal segment 2: male: 0.47 female: 0.51; antennal segment 1/antennal segment 3: male: 0.44 female: 0.56; antennal segment 1/antennal segment 4: male: 0.38 female: - ; rostral segments I–III lengths relationships: rostral segment I/rostral segment II: male: 0.58 female: 0.61; rostral segment I/rostral segment III: male: 1.00 female: 1.36; pronotum length: male: 2.15 female: 2.01; pronotal anterior lobule length/pronotal posterior lobule length: male: 1.5, female: 1.19.

Distribution.—Afrotropical: Guinea and Zaire.

Material studied.—Holotype male, Nion, Muséum Paris, Nimba (Guinée), M. Lamotte II-VI-1942, *Rapites elongatum* A. Villiers det. (Museúm National d'Histoire Naturelle, Paris, France). Holotype female, *Rapites villiersi*, Musée du Congo, Kivu, Mabulta XII-1935 Boutakoff, R. Det. R., 4949, *Pirates* n. sp. n. gen. A. Villiers det., *Rapites villiersi* Sch. Type (Instituut voor Taxonomisch Zoologisch Museum, Amsterdam, The Netherlands).

Remarks.—I consider *Rapites elongatus* and *R. villiersi* as synomyms. I agree with Schouteden (1952) that the only differences between these species are the coloration of antennal segments I and II (in the male only dark brown) and the color pattern of the conexivum. Both of the characters are variable and, in my opinion, do not distinguish species. Previous observations performed within the subfamily Peiratinae demonstrated that these characters may show intraspecific variation (Coscarón 1994b, Coscarón and Carpintero 1994, Coscarón and Morrone 1995).

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tomology from the Zoological Museum of the University of Helsinki for their help and assistance.

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A NEW *GLYPHOPSYCHE* BANKS (TRICHOPTERA: LIMNEPHILIDAE) FROM SOUTHEASTERN TENNESSEE

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Abstract.—***Glyphopsyche sequatchie* Etnier and Hix, new species**, is described from Owen Spring Branch, Sequatchie, Marion County, Tennessee. The male differs from the other two species in the genus, *G. irrorata* and *G. missouri,* in having far more elaborate genitalia and in having two rather than three patches of black spines on the dorsum of segment 8. Adult females, pupae, and larvae are also easily separable from these species. A second population of *Glyphopsyche,* known from two larvae collected on 9 May 1998 from Martin Spring run, 12.0 air miles WNW of the type locality, was confirmed as representing the same species based on adults reared in November 1998. *Glyphopsyche* larvae have not been found in other spring-type habitats in the area, and *G. sequatchie* has been recommended for protected status under the Endangered Species Act.

Key Words: Trichoptera, Limnephilidae, *Glyphopsyche,* Tennessee, spring habitats, endangered species

On 21 March 1994, the junior author collected a single limnephilid larva from Owen Spring Branch in Sequatchie, Marion County, Tennessee, that appeared to represent the distinctive genus *Glyphopsyche* Banks (Trichoptera: Limnephilidae). As this genus is currently known to contain only the boreal *G. irrorata* (F.) and *G. missouri* Ross, a species restricted to Meramec Springs, St. James, Phelps County, Missouri, the find created considerable excitement. We subsequently reared numerous adults from pupae and last instar larvae collected from Owen Spring Branch.

On 9 May 1998, the senior author collected two *Glyphopsyche* larvae from Martin Spring, 7620 Martin Springs Road, 12.0 air miles WNW of Owen Spring. Pupae/prepupae were collected from Martin Spring on 25 October 1998, and adults reared from these were found to be conspecific with those from Owen Spring. These Tennessee *Glyphopsyche* differ trenchantly from the two nominal species in characteristics of the male and female genitalia, pupae, and larvae, and are described below as a new species.

Glyphopsyche sequatchie Etnier and Hix, new species

(Figs. 1, 2)

Types.—Holotype ♂, Owen Spring Branch, Old Tennessee Highway 28, Sequatchie, Marion County, Tennessee, collected 27 September 1996, D. A. Etnier, emerged 31 October 1996; deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Allotype ♀, same data, emerged 11 December 1996 (USNM). Paratypes, all collected with the holotype: USNM, ♂, emerged 31 December 1996; Clemson Uni-

versity, ♂, emerged 11 November 1996; Illinois Natural History Survey, ♂, emerged 7 November 1996, ♀, emerged 14 January 1997; Royal Ontario Museum 27361, ♂, emerged 11 November 1996; California Academy of Sciences (Ex UT 7.447), ♂, emerged 31 December 1996; University of Tennessee 7.448, ♂, 2 mature ♀ pupae, preserved 13 January 1997. Larval sclerites and pupal exuviae are included in all of the type lots. Larvae collected at the type locality on 3 June 1995 have been deposited in all of the above repositories.

Additional specimens examined.—Martin Spring run, J. K. Kelly property, 7620 Martin Springs Road (just east of I-24, Martin Springs exit), Battle Creek system, Marion County, Tennessee: 9 May 1998, 2 larvae, UT 7.495; 25 October 1998, 16 pupae/prepupae, 14 of which emerged as winged adults or mature pupae that failed to complete the final ecdysis, 6–20 November 1998, 7 ♂, 7 ♀. A male and female (imago or mature pupa) have been deposited with each of the following: A. P. Nimmo collection, Carnegie Museum of Natural History, Marshall University, Ohio State University Museum of Biological Diversity, S. C. Harris collection, University of Minnesota, and UT 7.506.

Diagnosis.—Separable from males of both nominal species of *Glyphopsyche* in (1) having two rather than three patches of black spinules on the posterior margin of the eighth abdominal tergite (Fig. 1a); (2) having an elongate projection on the inferior appendage of segment 10 (Figs. 1a, b, 2a); (3) having three pairs of elongate sclerotized dorsal and intermediate processes (Figs. 1a, b, 2a) on segment 10 (versus 2 pairs of short processes); (4) having the length of the phallic parameres (Figs. 1c, d) more than twice the diameter of the phallus versus subequal to the diameter of the phallus; and (5) virtually lacking a partial crossvein between veins Sc and R1 at the cord (Fig. 2) versus with a crossvein extending from Rs more than halfway to Sc. Characters that appear to be diagnostic for the female, pupa, and larva appear in their descriptions.

Description.—*Adult male:* Length 18 mm. Head yellow with yellow warts slightly lighter in color than remainder of head. Setae on head yellow to light brown unless otherwise indicated. Two oval warts, each bearing about five setae, located between each lateral ocellus and anterior ocellus; two more linear warts, each bearing four or five setae, located slightly posterior and medial to lateral ocelli. Occiput with a pair of large, oval warts medially, each with about 15 setae, and another pair laterally behind eyes, each with about 20 dark brown setae. Labial and maxillary palpi yellow; length of middle (longest) segment of three-segmented maxillary palp subequal to diameter of eye. Antenna yellow at base and grading to black at tip, with about 60 segments. Antenna and palpi clothed with appressed brown setae. Front of head with two oval warts along inner margin of each eye, each with about 12 setae, and with a linear wart on each side of midline with about 20 setae. Labrum with a transverse cluster of setae across middle.

Thoracic sclerites and associated warts and setae yellow, with warts paler yellow. Legs yellow, grading gradually to brown distally on tarsi, except fore leg brown on tarsus, dorsal margin of tibia, and ventral margin of femur. All legs with fringes of yellow setae on coxae and with black spines forming two irregular rows on tibiae and two well defined rows on tarsi. Fore and middle femora each with a single black spine distally. Fore tibia (the following counts based on five males) with 4–7 black spines; middle tibia with 21–26 black spines; hind tibia lacking black spines on proximal third and with 12–14 black spines on distal two-thirds. Proximal (first) tarsal segment with 5–9 black spines on fore leg and 20–27 black spines on middle and hind legs. Second tarsal segment with 4, 12–20, and 10–15 black spines on fore, middle, and hind legs, respectively. Third tarsal segment with 3–4, 9–10, and 7–11 black

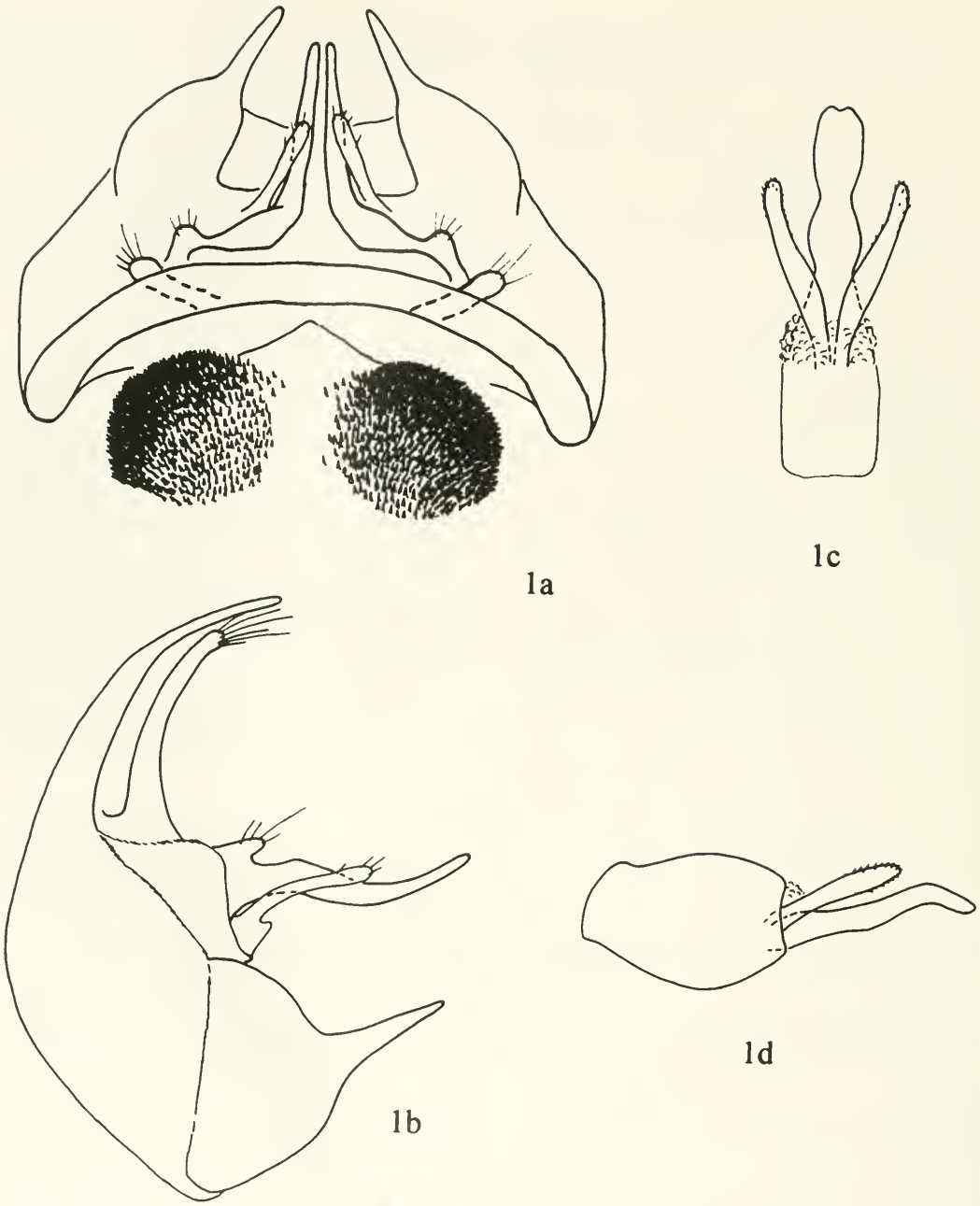

Fig. 1. *Glyphopsyche sequatchie*, male genitalia (setae on inferior appendage not shown). a, Dorsal view. b, Lateral view. c, Phallus, dorsal view. d, Phallus, ventral view.

spines on fore, middle, and hind legs, respectively. Fourth tarsal segment with 2 black spines on fore leg and with 4 black spines on middle and hind legs. Distal (fifth) tarsal segments lacking black spines. Tibial spurs 1, 2, 2. Tibial spurs and tarsal claws yellow.

Fore wing clear yellow anterior to vein Rs, purple/brown at stigma, clothed with yellow setae anterior to vein Rs and with

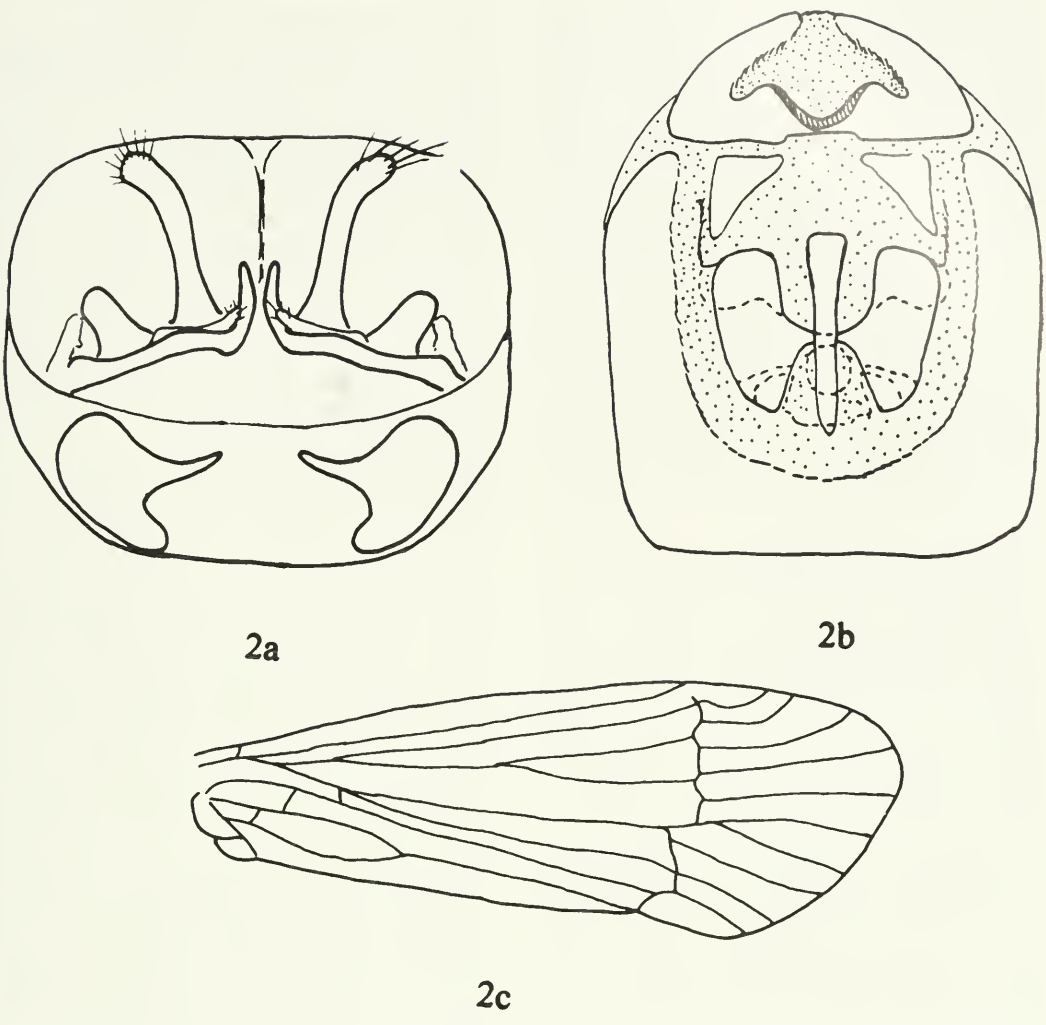

Fig. 2. *Glyphopsyche sequatchie.* a, Male genitalia, caudal view. b, Female genitalia, ventral view (setae not shown). c, Forewing.

dark brown setae elsewhere. Remainder of forewing irrorate purple/brown on yellow background, with darker pigment concentrated in anal area and just distal to cord in two cells between veins R4 and M1. Veins yellow, those distal to the cord with alternating dark markings, especially on R3–R5 and M1.

Adult female: Length 20 mm. Differs from male as follows: Head about one-third larger but eyes same size. Maxillary palpus five-segmented, with second and third segments longest, subequal, and about three-fourths of eye diameter. All legs yellow basally and grading gradually to brown distally. Fore tibia (5 females counted) with 11–17 black spines (only 4–7 in male). Female genitalia (Fig. 2b) with median process on subgenital plate on ventral portion of segment VIII expanded at tip and with lateral processes rounded distally (in *Glyphopsyche irrorata* and *G. missouri* median process not expanded at tip, and lateral processes truncate distally (Ross 1944: 200, fig. 692D; Schmid 1980: 249, fig. 465.

Last instar larva: Typical for *Glyphopsyche* as described by Flint (1960) and Wiggins (1996). Length 16–18 mm (14 mm in

G. missouri, 15–17 mm in *G. irrorata,* Flint 1960). Left mandible with four apical teeth, right mandible with three well developed and two poorly defined apical teeth. Legs as in *G. missouri,* with dark apical annuli on femora, tibiae, and tarsi. Gills much reduced relative to both *G. missouri* and *G. irrorata,* both in number and number of branches, with branched dorsal gills ending on segment IV and no dorsal gills posterior to V (branched dorsal gills through VII or VIII on other two species). Lateral gills unbranched and only on IIp and IIIa (often branched and on IIp through V (*G. missouri*) or IIp through VII or VIII (*G. irrorata*)). Ventral gills 3-branched only on posterior portions of II through IV (versus 3-branched on both anterior and posterior positions from IIp through Vp and on VIp). Actual gill counts from four larvae as follows, arabic numerals indicate number of branches and anterior and posterior gill counts separated by a comma: Dorsal—II 1–2, 3–4; III 3, 3; IV 1–2, 1–2; V 1, 0–1; lateral—II 0, 1; III 0–1, 0; ventral—II 0–1, 3; III 1–2, 3; IV 1, 2–3; V 1, 1–2; VI 0–1, 1–2; VII 0, 0–1. Chloride epithelium (= ventral rings of Flint 1960) present on segments III–VII, as indicated for *G. irrorata* by Flint (1960) and Wiggins (1996). (We noted a small, often nearly circular patch of chloride epithelium on venter of abdominal segment VIII in all ten larvae of *G. missouri* examined.) As in *G. missouri,* cases extremely variable, ranging from 100% vegetation to 100% mineral, but tending to have higher proportions of vegetation than in *G. missouri.*

Pupa: Based on examination of three pupae each of *G. sequatchie* and *G. missouri*; pupae of *G. irrorata* not seen. Length 16–18 mm (12–14 mm for *G. missouri*). Mandible with swollen base and distal blade that lacks serrations. Labrum with two clusters of five short, stout black setae that appear to have been clipped off at their ends, these setae slightly shorter than vertical height of base of mandible (these setae more than twice as long as vertical height of base of mandible in *G. missouri,* and with their pointed tips bent mesad at right angles). Middle coxa with a black ventral seta at anterior and posterior fourth (middle coxa with a patch of three to five black setae at midlength in *G. missouri*). Proximal four middle tarsal and hind tarsal segments with two dense rows of swimming hairs, these hairs subequal in length to segment on which they occur. Dorsum of abdominal segment I with a median bilobed region that bears sclerotized teeth on its posterior margin. Dorsal hook-bearing plates on abdominal segments Vp, and IIIa through VIIa, those on Vp transverse and with 10–15 hooks loosely arranged into an anterior and posterior row (only 8–12 hooks in *G. missouri*); plates on anterior portions of segments all similar in size, nearly circular, and typically with 3 (2–4) hooks per plate (plate on IIIa absent to weakly developed and linear, with only 1 or 2 hooks in *G. missouri*). Gills (see larval description for explanation of formulae): Dorsal—II 1, 2–3; III 2–3, 2–3; IV 1–2, 1; V 0–1, 0–1; lateral—II 0, 1; III 0–1, 0; ventral—II 0–1, 1–3; III 2–3, 2–3; IV 1, 1–3; V 0–1, 2; VI 0–1, 1–2; VII 0, 1. Gills for *G. missouri:* Dorsal—II 0–2, 2–3; III 3, 3; IV 3, 3; V 2–3, 0–2; VI 1–2, 0–2; VII 0–1, 0; lateral—II 0, 2–3; III 2, 2–3; IV 2–3, 1; V 1–2, 0–1; ventral—II 0–2, 3; III 3, 3; IV 2–3, 3; V 2–3, 3; VI 2, 2–3; VII 0–1, 1–2. Gills much more profuse on *G. missouri,* with lateral gills often branched and extending from IIp through Va, and with segments IV and V with 20+ gill branches per segment; in *G. sequatchie* lateral gills single and only on IIp and IIIa, and segments IV and V have 12 or fewer gill branches per segment. Since *G. irrorata* larvae have gills even more profuse than those of *G. missouri,* and pupal and larval gill formulae appear to be identical, above differences may also separate pupae of *G. sequatchie* and *G. irrorata.*

Etymology.—The species epithet is a noun in apposition, referring both to the type locality in the city of Sequatchie, and

to the rich aquatic fauna of the Sequatchie River system.

Habitat and biological notes.—Owen Spring emerges from a cave mouth about 200 m west of Old Tennessee Highway 28 in Sequatchie, Marion County, Tennessee. The spring run averages about 12 m wide by 0.5 m deep and flows over substrates of chert gravel, with silt and organic detritus in the pool areas. A small park, owned by the State of Tennessee, surrounds the spring and spring run. About 15 m above Old Hwy. 28 the spring run is joined by a distributary of Little Sequatchie River called The Lagoon to form Owen Spring Branch. Owen Spring Branch acquires another first order tributary prior to entering Little Sequatchie River about 1.3 creek km (0.8 miles) below Owen Spring. *Glyphopsyche* larvae occur in the spring run from about 30 m below the mouth of the cave downstream at least to about 150 m below Old Hwy. 28, a reach of about 300 m. At this point there is a sawdust pile in Owen Spring Branch from a lumber operation that produces hickory handles for hand tools. Larvae were becoming increasingly difficult to find in this area, and the search for larvae was terminated at the sawdust pile. No *Glyphopsyche* larvae were found in the noticeably warmer waters of The Lagoon.

Larvae were large enough to be identified with ease by early June, and were in final instar in early September. Ten larvae collected on 1 September 1996 were returned to the University of Tennessee and were reared in individual 8-oz jars in an incubator at 18° C, 12 h light/12 h dark. When these showed no inclination to pupate, an additonal collecting trip was made on 27 September. On that date, 50 last instar larvae and 5 pupae or prepupae (anterior end of case closed) were found by the senior author in an exhaustive search throughout the reach occupied by *Glyphopsyche*. Most larvae were found in pools or gently flowing runs on dead limbs 5–10 cm in diameter with bark still attached. Additonal larvae were found on larger logs, with and without bark, and in wads of root hairs. The occasional boulders in the reach were not used by *Glyphopsyche* larvae. Nine of these larvae and the five prepupae were kept for rearing. These larvae were occasionally removed from their 8-oz jars and placed in a shallow pan of spring water with crumbs of dry dog food provided. Many of the larvae fed eagerly, and they were allowed to feed about a half day before being returned to their individual jars. All of the larvae collected on 1 September died before pupating. All but one of the larvae collected on 27 September survived to adulthood (9) or to become mature pupae that exited their larval case but failed to complete their final molt (4).

Emergence dates extended from 31 October through 4 February. While this extended late fall and winter emergence may be an artifact of laboratory rearing, we suspect that a similar emergence pattern might prevail under natural conditions. The boreal *Glyphopsyche irrorata* is known from adults throughout the winter months (Nimmo 1970, Wiggins 1996) and they apparently overwinter as adults. Ross (1944), suggested that emergence of *G. missouri* is concentrated in early October. The sample of *G. missouri* we have seen from 3 September includes mature pupae as well as mid-instar larvae, suggesting that emergence extends considerably later into the fall and perhaps into winter.

On 9 May 1998 a second population of *Glyphopsyche* was located 12.0 air miles (19.3 air km) WNW of the type locality by DAE. This locality, Martin Spring run at the J. Kenneth Kelly residence, 1620 Martin Springs Road, is on the east side of Interstate 24, 1.4 road miles northwest of the Martin Springs exit, Marion County, Tennessee. The spring run emerges from a cave about 300 m above the Kelly residence, and has approximately twice the width and discharge of Owen Spring run. Although only two *Glyphopsyche* larvae were found in a half-hour search, the amount of apparently suitable habitat is several times greater than

at Owen Spring. On 25 October 1998 17 pupal cases (one had already emerged) were found in about 1 hour of effort and returned to the laboratory for rearing. Fourteen of these (seven males, seven females) emerged from 5–20 November as imagos or mature pupae. Adults, pupae, and larvae from this site are not separable from those from Owen Spring, except that the crossvein (see Diagnosis) at the cord between Rs and Sc is barely detectable.

Status.—Etnier (1997) listed sites in the vicinity of Owen Spring that had been unsuccessfully searched for populations of *Glyphopsyche,* but indicated that additional springs in the area needed to be examined. The 9 May 1998 discovery of a second and apparently much larger population of *G. sequatchie* causes the species' status to be much less imperiled than originally believed, and justifies some optimism that additional populations may exist in the many springs in the lower bend of the Tennessee River. At this time it does not seem likely that enough additional populations will be found to change our opinion that *G. sequatchie* deserves protection under the Endangered Species Act as an endangered or threatened species.

Long term protection of the Owen Spring type locality would also protect one of only three known populations of the endangered royal springsnail (*Pyrgulopsis ogomorphae* Thompson) located by Gordon (1991). During the 27 September 1996 collection, I (DAE) attempted to locate all of the *Glyphopsyche* larvae in the approximatley 300 m reach of Owen Spring Branch where they were known to occur. If the total of 55 individuals located in about three hours of effort represents somewhere between one and ten percent of the population, as seems reasonable, the total population that could be expected to survive to adulthood would be somewhere between 500 and 5,000. Thus, the known population is probably tiny to moderate, and trichopterists are urged to treat this population as endangered until such time as official protection is afforded it. The population in Martin Spring is estimated (by DAE, based on two brief visits) to be some two to ten times higher than that of Owen Spring Branch.

Acknowledgments

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REVISION OF THE *COLOMBIANA* SPECIES GROUP OF THE GENUS *HEXACHAETA* LOEW (DIPTERA: TEPHRITIDAE)

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Abstract.—The *colombiana* species group of the Neotropical genus *Hexachaeta* Loew is revised. The group includes one described species, *H. colombiana* Lima 1953 and four new species: ***H. ecuatoriana***, ***H. leptofasciata***, ***H. bifurcata***, and ***H. nigriventris*** from several regions of tropical America. A key for separation of all species is presented, and the most important characters for distinguishing each species are illustrated.

Resumen.—En este estudio se hace una revisión de las especies del grupo *colombiana* comprendidas en el género neotropical *Hexachaeta* Loew. Este grupo incluye una especie descrita, *H. colombiana* Lima, y cuatro especies nuevas para la ciencia: ***H. ecuatoriana***, ***H. leptofasciata***, ***H. bifurcata***, y ***H. nigriventris,*** las cuales proceden de varias regiones tropicales de América. Se presenta una clave para la separación de todas las especies y se describen e ilustran los caracteres más importantes que distinguen a cada una de ellas.

Key Words: *Hexachaeta, colombiana* group, new species

Currently the genus *Hexachaeta* Loew is recognized as a group exclusively distributed in America and mainly in the Neotropics. This genus comprises 25 described species, to date recorded from the southern United States (southern Texas) to Argentina (Foote 1967).

Hexachaeta belongs to the subfamily Trypetinae, but its tribal affinities are not clear. Some authors such as Foote (1980), have discussed its possible relationship with the Old World tribe Acanthonevrini, and other American genera such as *Blepharoneura* Loew, *Ceratodacus* Hendel, *Pyrgotoides* Curran, and *Ischyropteron* Bigot, mainly based on the presence of a plumose arista and/or six scutellar bristles.

Hexachaeta lacks other diagnostic characters of the tribe Acanthonevrini such as an aculeus tip not fused, spermathecae without denticles on surface, and subapical tactile setae in the aculeus tip (sensu Hancock 1986). Extreme reduction of ocellar bristles is also present in some *Hexachaeta* species.

In recent studies analyzing ribosomal mitochondrial DNA (16S) in diverse tephritid species (including *H. amabilis* (Loew)), Han and McPheron (1997) have proposed that *Hexachaeta* has a close phylogenetic relationship with the tribe Toxotrypanini (sensu Foote et al. 1993) which comprises the genera *Anastrepha* Schiner and *Toxotrypana* Gerstaecker. Han and McPheron's (1997) hypothesis reconfirms the monophyly of the Toxotrypanini and suggest that the genus *Hexachaeta* is a possible sister group of the tribe.

Loew (1873), Hendel (1914), Lima (1935, 1953a, 1953b, 1954), and Lima and Costa Leite (1952) have made the most extensive taxonomic work in *Hexachaeta*, and

they described most of the currently known species.

To date, the infrageneric classification of *Hexachaeta* has not been well understood. Lima (1935) recognized two species groups, the first that he denominated *amabilis* including the species *H. amabilis, H. obscura* Hendel, and later *H. shannoni* Lima (Lima 1953a); and a second group named only "group 2," distributed into "two divisions," but the characters that define each one of them were used with ambiguity.

At the moment, this genus is being revised in a general context, using characters of male and female terminalia that previously were not used for their classification (Hernández-Ortiz, in prep.).

In this study I describe the *colombiana* species group based on the revision of specimens from diverse regions of the Neotropics. It includes *H. colombiana* and four closely related new species which are recognized mainly on the basis of differences in their female terminalia.

Material and Methods

Specimens from various countries of Central and South America were examined and their terminalia dissected and stored following the technique described by Gurney et al. (1964). Acronyms used in the text belong to the institutions where study material is deposited: CAS, California Academy of Sciences, San Francisco, USA; CNC, Canadian National Collection Ottawa, Canada; FML, Fundación Miguel Lillo, Tucumán, Argentina; IEXA, Instituto de Ecología, Xalapa, México; INBIO, Instituto Nacional de Biodiversidad, Costa Rica; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; USP, Universidade de São Paulo, São Paulo, Brazil.

Nomenclature for the general morphological terminology of adults follows McAlpine (1981), whereas that for the female terminalia follows Norrbom and Kim (1988), and for the wing pattern Foote (1981).

The *Colombiana* Species Group

Description.—*Head:* Ocellar bristle usually well developed (at least as long and strong as postocellar bristle); postocellar bristle black or reddish brown; fascial carina very reduced or inconspicuous.

Thorax: Scutum yellow or pale reddish, and usually without blackish bands or stripes including posterior margin; scutellum usually of same color of scutum; mediotergite yellow or reddish; dorsocentral bristle located near midpoint between supra-alar and postalar bristles.

Wings: Posteroapical extension of cell cup moderately long but less than one half length of main part of body of cell. Vein Cu with dorsal microsetae present (usually before fork of Cu1 and Cu2); distance between r-m and dm-cu less than length of dm-cu; vein r-m located distal to level of apex of R1. Radial cells with two elongate hyaline marks distal to apex of R1, first extended into br, and second usually extended to inferior wing margin or at least well introduced into discal cell (Figs. 1A–E); anterior apical band discrete broad or slender (3–4 times as broad as costal vein); posterior apical band present; discal and subapical bands usually separated along entire length but sometimes joined along vein Cu1 or posterior to it; basal third or more of discal cell with a broad hyaline mark occupying entire width; cell bm broadly hyaline.

Abdomen: Tergites usually yellowish but sometimes with some lateral black spots on last segments or exceptionally entirely blackish (as in *H. nigriventris,* n. sp.).

Female terminalia (Figs. 2A–H, 3A–B): Aculeus always shorter than length of syntergosternite 7 (approximately 0.4–0.7 times its length); aculeus tip nonserrate; usually simple or bilobed at end (as in *H. bifurcata,* n. sp.), and usually with a sharply narrowed area in which there is often a step-like bend in lateral margin.

Male terminalia (Figs. 3C–D): Proctig-

er with a sclerotized region ventrally; outer surstylus very elongate and curved posteriorly, apex hook shaped dorsally; inner surstylus half as long as outer surstylus; with two short toothlike well defined prensisetae.

Diagnosis.—Ocellar bristle well developed; base of vein Cu always covered with at least a few microsetae on dorsal surface; setulae on disk of scutellum always present; apex of aculeus tip simple or bilobed, lateral margin nonserrate but usually with a sharply narrowed area. Most of these characters are shared only with species like *H. eximia* (Wiedemann), *H. dinia* (Walker), *H. enderleini* Lima, *H. seabrai* Lima, and others related under "first division" (see Lima 1953b). However, the species of the *colombiana* group differ from these by the presence of a ventral sclerite on the base of proctiger's male; while the second hyaline mark in cell r1 usually extends to the inferior margin of wing, meaning that the discal and subapical bands are completely separated, or sometimes they are weakly connected on vein CuA1 or posterior to it.

Remarks.—The *colombiana* species group is widely distributed from southern Mexico (Chiapas) to Argentina, but most of the known species occur in northern South America (Colombia, Venezuela, and Ecuador). To date we have no information about their host plants.

Key to Species of the *Colombiana* Group

1. Abdominal tergites entirely yellow or sometimes with small lateral blackish spots on tergite 5 in male or 6 in female; syntergosternite 7 yellow or dark brown; aculeus tip variable 2
– Abdominal tergites entirely brownish black, including syntergosternite 7; aculeus tip (Figs. 2E–F) with a pronounced narrowing on each side forming an angle less than 90°, part apical to narrowing very short and slender . . . . . *H. nigriventris*, n. sp.
2. Aculeus tip (Fig. 2A–B) simple, without sharp narrowing on lateral margins and gradually tapering to apex; wing pattern (Fig. 1B) with discal and subapical bands joined in cell cu1 . . . . . *H. colombiana* Lima
– Aculeus tip (Figs. 2C–D, G–H, 3A–B) sharply narrowed, with distinct bend on lateral margin; wing pattern (Figs. 1A, C–D) with discal and subapical bands always completely separated 3
3. Apical extreme of aculeus tip bilobed; aculeus extremely short, less than half length of syntergosternite 7 (Figs. 2G–H) . . . . . *H. bifurcata*, n. sp.
– Apical extreme of aculeus tip simple; aculeus always longer than half length of syntergosternite 7 4
4. Wing pattern (Fig. 1D) with bands extremely slender, subapical band (along vein dm-cu) similar in width to anterior apical band; aculeus tip (Figs. 3A–B) very sharply narrowed with angle of approximately 90° on lateral margin at narrowed area. . . . *H. leptofasciata*, n. sp.
– Wing pattern (Fig. 1C) with bands broader, subapical band (along vein dm-cu) two times as broad as anterior apical band; aculeus tip (Figs. 2C–D) with less pronounced narrowed area, with angle of more than 100° in lateral margin . . . . . *H. ecuatoriana*, n. sp.

Hexachaeta colombiana Lima

(Figs. 1B, 2A–B, 3C)

Hexachaeta colombiana Lima 1953b: 560 (original description, wing, genitalia); Foote 1967: 26 (in Neotropical catalog).

Type material.—Holotype ♂ USNM (examined): COLOMBIA, Cundinamarca, 1933, L.M. Murillo. 2 slides #10 USNM wing + terminalia of male.

Material examined.—COLOMBIA: Anolaima, XI-1977, McPhail trap (3♂, 2♀ USNM); Santander del Sur, Barbosa 1530 m, 3-VIII-1994, E. Molina col. (4♂, 10♀ IEXA); COSTA RICA: Cártago, Chirripo, Turrialba, Grano de Oro 1120 m, IX-1992, P. Campos L-N 200250, 595900 (1♂ INBIO CRI000918933); Prov. Puntarenas, Jardín Las Cruces, 6 Km S San Vito on Rt 16, 29-V-1987, McPhail trap, A.L. Norrbom & R. Mexzon (1♂, 1♀ USNM).

Description.—*Head:* 1.32–1.8 mm high, 0.88–1.2 mm wide in lateral view; ocellar bristle well developed (at least as long as postocellar bristle); postocellar seta brownish black; arista only with sparse short hairs on apical third.

Thorax: Mesonotum 2.46–2.59 mm

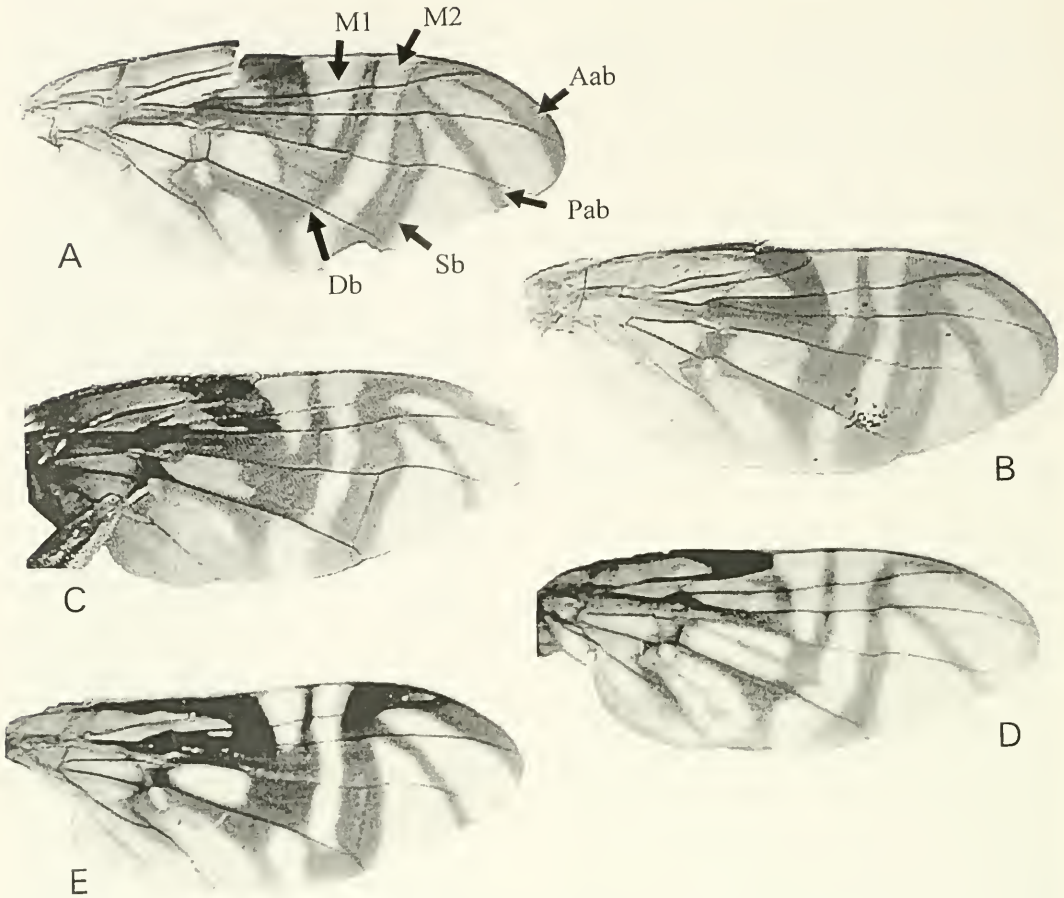

Fig. 1. Wing pattern of species of the *Hexachaeta colombiana* group and nomenclature used in text. A, *H. bifurcata*. B, *H. colombiana*. C, *H. ecuatoriana*. D, *H. leptofasciata*. E, *H. nigriventris*. M1 = first hyaline mark (or proximal); M2 = second hyaline mark (or distal); Db = discal band; Sb = subapical band; Aab = anterior apical band; Pab = posterior apical band.

long; scutum completely yellow and covered by setulae of same coloration extending onto disc of scutellum; margins of scutellum slightly paler yellow than disc; pleuron sclerites, subscutellum and mediotergite entirely yellow; legs yellow.

Wing (Fig. 1B): Length 5.6–6.84 mm; costal cell mostly yellow; bands of wing pattern brownish black with two hyaline markings in cell r1; first (proximal) extended to or almost to vein M, and second (distal) broadly projected into discal cell; discal and subapical bands joined only on vein CuA1 and in cell cu1; vein Cu covered by some dorsal microsetae to level of fork of Cu1 and Cu2; basal third of discal cell broadly hyaline; abdominal tergites completely yellow.

Male terminalia (Fig. 3C): Epandrium mostly brownish black; proctiger relatively short and with a conspicuous ventral sclerite basally; outer surstylus strongly curved posteriorly, dorsally with a small preapical hook; inner surstylus broad and half as long as outer surstylus; two prensisetae tooth-shaped, short, but well developed.

Female terminalia: Syntergosternite 7 brownish black, contrasting with yellow abdominal tergites, length 1.9–2.19 mm, approximately as long as total length of pre-

abdomen; aculeus (Figs. 2A–B) 1.24–1.43 mm long, tip simple, tapering gradually to apex without any sharp angles in lateral margin.

Distribution.—Colombia, Costa Rica.

Remarks.—This species was previously known only from the holotype male, and the female terminalia is described here for the first time. The Costa Rican specimens show some variation in the wing pattern because the anterior apical band is broader than in the rest of material examined, but all characteristics of the aculeus are similar, showing that these specimens are conspecific.

Hexachaeta ecuatoriana Hernández, new species

(Figs. 1C, 2C–D, 3D)

Type material.—Holotype ♀ CNC: ECUADOR, Quitasol R. 50 km SW Quito, 2400 m, Pichincha, 24-25-II-65, Peña (teneral female). Paratypes: Same data as holotype (1♀ teneral CNC); Pimo (N Cañar) 3200 m, XII-1970, L.E. Peña col. (1♂ USP).

Description.—Female: *Head:* Yellow, 1.72–1.96 mm high and 1.12–1.24 mm wide in lateral view; frons reddish; ocellar bristle long and well developed (longer than postocellar bristle); postocellar bristle black; fascial carina poorly differentiated; arista bare on basal two thirds, apical third with some short and scarse hairs; genal bristle reddish.

Thorax: Mesonotum 3.06–3.21 mm long; scutum uniformly reddish brown extending this coloration into disc of scutellum; setulae of scutum and scutellum brownish uniformly distributed; pleuron sclerites, mediotergite and legs completely yellow.

Wing (Fig. 1C): 8.16–9.0 mm long, with a pattern of dark brown bands, with costal cell yellow as well as most of cells bm and cup; discal and subapical bands separated along entire length but relatively close together because subapical band broader than in other species; anterior apical band at least two times broader than posterior apical band, and close to vein M. First hyaline marking in cell r1 projecting slightly beyond vein R4+5 but not reaching vein M; base of vein Cu with 9–10 microsetae on dorsal surface but not extending beyond fork of Cu1 and Cu2.

Abdomen: Tergites completely yellow, including syntergosternite 7, except its apical extreme a little darker; syntergosternite 7, 1.94 mm long; aculeus (Fig. 2C–D) 1.15 mm long (0.59 times as long as syntergosternite 7), tip tapering gradually, then more rapidly near midlength, to simple apex.

Male: Similar to female but with abdominal tergites 3–5 pigmented with a brownish-black spot on each side gradually widening to posterior segments; epandrium reddish; proctiger with a sclerotized plate ventrally. Outer surstylus long and curved posteriorly (Fig. 3D); inner surstylus reaching mid length of former, with two prensisetae short, toothlike and well developed.

Etymology.—The specific name is derived from the country of origin of the type material.

Hexachaeta bifurcata Hernández, new species

(Figs. 1A, 2G–H)

Type material.—Holotype ♀ IEXA: MEXICO, Chiapas, Región del Soconusco (no date of collection). 2 slides, wing and abdomen + aculeus prep. IEXA Hex-09.

Description.—Female: *Head:* Yellow, 1.76 mm high and 1.20 mm wide in lateral view; most macrosetae lost, but due to large socket of ocellar bristle, apparently long and well developed; fascial carina very poorly developed.

Thorax: Mesonotum 3.65 mm long; scutum reddish yellow without any dark marks; setulae of scutum reddish brown and covering entire surface; discal region of scutellum covered by setulae of same color; pleuron sclerites, mediotergite, and legs yellow.

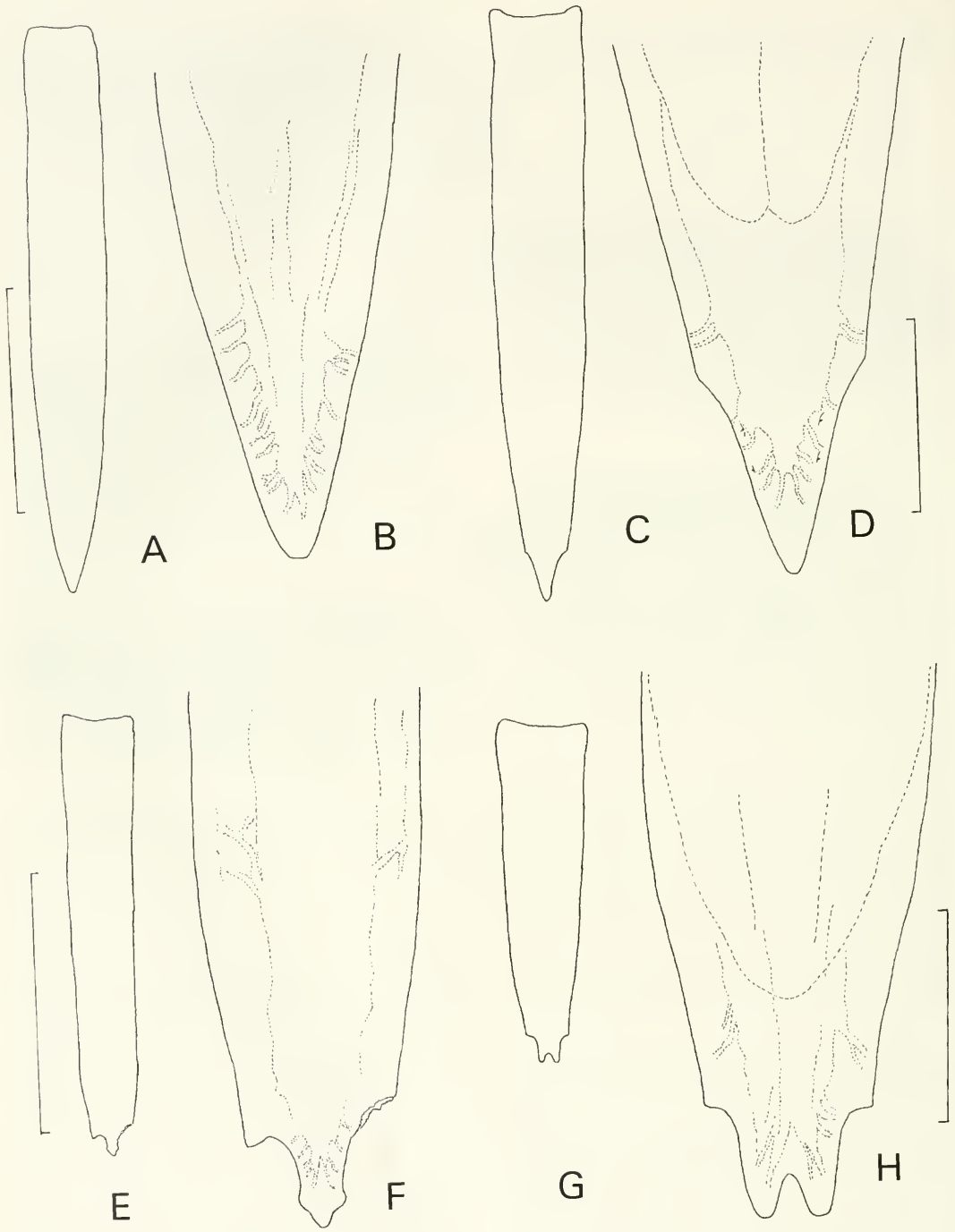

Fig. 2. Aculeus of *Hexachaeta* species, ventral view. A–B, *H. colombiana,* specimen from Colombia. C–D, *H. ecuatoriana,* holotype. E–F, *H. nigriventris,* holotype. G–H, *H. bifurcata,* holotype. A, C, E, G, general aspect of aculeus (line = 0.5 mm); B, D, F, H, aculeus tip (line = 0.1 mm).

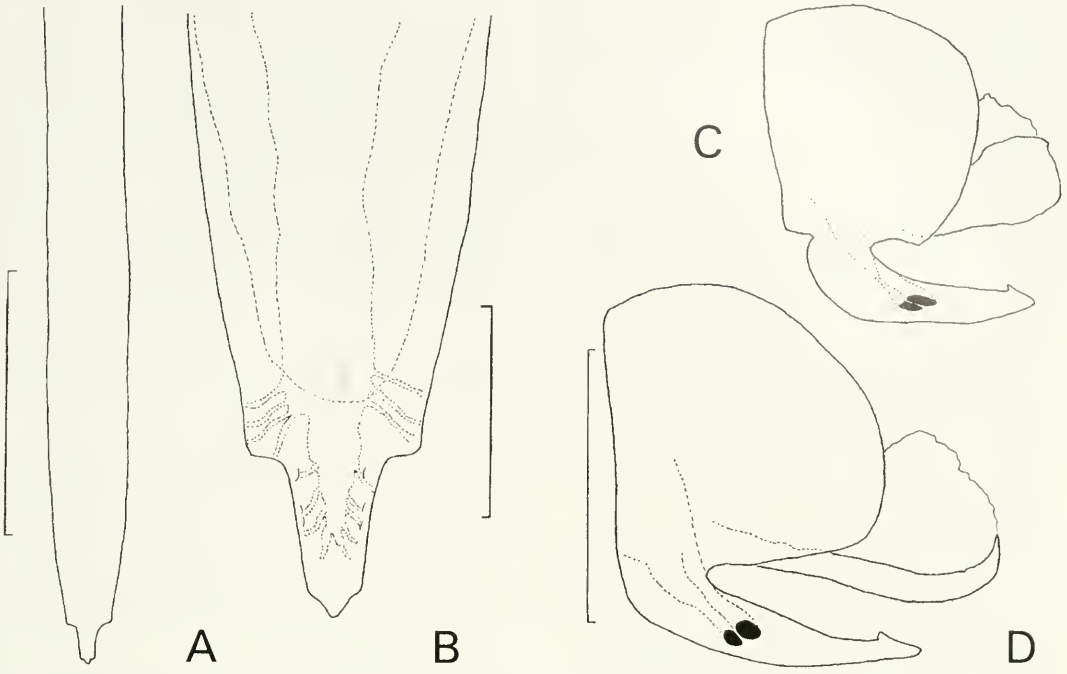

Fig. 3. Aculeus and male epandrium of *Hexachaeta* species. A–B, *H. leptofasciata*. A, general aspect of aculeus (line = 0.5 mm); B, aculeus tip (line = 0.1 mm). C, *H. colombiana*. D, *H. ecuatoriana*. C–D, male epandrium and surstyli in lateral view (line = 0.5 mm).

Wing: 8.42 mm long (Fig. 1A), with typical wing pattern of *colombiana* group; first hyaline marking in cell r1 reaching vein M, second hyaline marking extending to posterior margin of wing, thus discal and subapical bands completely separated; anterior and posterior apical bands present and moderately broad; base of vein Cu with 5–7 microsetae on dorsal surface and extending on to Cu1 to level of basal portion of discal cell.

Abdomen: Tergites mostly yellow or a little darker, with exception of segments 4 and 5 which have lateral blackish stripes that are larger on tergite 5. Syntergosternite 7 dark brownish, 1.60 mm long; aculeus (Figs. 2G–H) 0.62 mm long, extremely short (0.38 times as long as syntergosternite 7); aculeus tip near midlength with sharp turn in lateral margin of aproximately 90°, and with extreme apex bilobed.

Male: Unknown.

Etymology.—The name is derived from Latin in reference to the most important characteristic of the aculeus tip, unique among all known species of the *colombiana* group.

Hexachaeta nigriventris Hernández, new species

(Figs. 1E, 2E–F)

Type material.—Holotype ♀ CAS: VENEZUELA, El Avila, D.F. "El Lagunazo" Parque Nacional, 3-IX-1977, John E. Lattke, Cal. Acad. Sci. Coll./as *Hexachaeta colombiana* Lima, det. Norrbom.

Description.—*Female: Head:* Yellow, 1.68 mm high and 0.92 mm wide in lateral view, but with sides of ocellar triangle slightly darker; fascial carina poorly developed; ocellar bristles lost, but with large sockets so apparently well developed.

Thorax: Mesonotum 3.06 mm long; scutum reddish yellow covered by pale yellow setulae; scutellum disc with dark brownish

setulae; all sclerites of pleuron, legs, and mediotergite reddish yellow, without any dark or blackish marks.

Wing: 7.32 mm long (Fig. 1E), with blackish pattern of broad bands; costal cell with dark marking occupying nearly all of anterior mid length; first triangular hyaline mark in cell r1 reaching vein R4+5, second hyaline mark broadly extended into discal cell; discal and subapical bands slightly joined along vein CuA1; anterior apical band broader than posterior apical band but not reaching vein M; base of vein Cu with 10–11 microsetae dorsally; subapical band at least two times broader than posterior apical band.

Abdomen: All tergites uniformly brownish black; syntergosternite 7 dark brown, 1.77 mm long; aculeus (Fig. 2E–F) 0.83 mm long (0.46 times as long as syntergosternite 7); aculeus tip sharply narrowed, lateral margin with bend of less than 90°, forming shallow lobe (one side broken in holotype); apex slender and slightly notched, not bilobed.

Male: Unknown.

Etymology.—Derived from the Latin *nigrum,* relating to the black coloration of all abdominal tergites.

Hexachaeta leptofasciata Hernández, new species

(Figs. 1D, 3A–B)

Type material.—Holotype ♀ FML: ARGENTINA, Salta, Dpto. Orán, Ruta nac. 57 km 21 "El Chorro" 1,130 m, 28-X-1978, Col. P. Fidalgo.

Description.—*Female: Head:* Uniformly reddish, 1.64 mm high and 1.20 mm wide in lateral view; frons slightly darker on anterior half; ocellar bristle well developed, at least as long as postocellar bristle which is reddish brown; arista with short pilosity on apical half; genal bristle reddish.

Thorax: Mesonotum 2.96 mm long; scutum uniformly reddish brown and covered by yellow setulae extending onto disc of scutellum; sclerites of pleuron, mediotergite, and all legs reddish yellow without any dark markings.

Wing (Fig. 1D): 7.24 mm long, with bands well defined but conspicuously more slender than in other species of *colombiana* group; discal and subapical bands completely separated; discal cell with a broad hyaline marking at base extending to or almost to level of crossvein r-m; costal cell broadly hyaline; anterior apical band slender, not reaching vein M, approximately as broad as posterior apical band; base of vein Cu dorsally with 6–7 microsetae.

Abdomen: All tergites entirely yellow; syntergosternite 7 dark brownish, 1.99 mm long; aculeus (Figs. 3A–B) 1.44 mm long (0.72 times length of syntergosternite 7); aculeus tip sharply narrowed at basal ¼, with bend in lateral margin of near 90°, apex slender with notches, not bilobed.

Male: Unknown.

Etymology.—From the Latin *leptos* = slender and *fascia* = bands in reference to the slender wing bands of this species.

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HYPERPARASITISM BY *ABLERUS CLISIOCAMPAE* ASHMEAD (HYMENOPTERA: APHELINIDAE)

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Abstract.—*Ablerus clisiocampae* (Hymenoptera: Aphelinidae) is known as a parasitoid both of diaspidid scale insects and lepidopteran eggs. Although it has been suspected that *A. clisiocampae* is a secondary (hyper) parasitoid of diaspidid scale insects, direct evidence of hyperparasitism has been lacking. We used observation and rearing data from field-collected material to demonstrate hyperparasitism of three species of diaspidid scale insects, and primary parasitism of two species of parasitoid wasps by *A. clisiocampae*. *Ablerus clisiocampae* was found feeding on *Aphytis aonidiae* (Hymenoptera: Aphelinidae) attacking San Jose scale (*Quadraspidiotus perniciosus*) and *Comperiella bifasciata* (Hymenoptera: Encyrtidae) attacking California red scale (*Aonidiella aurantii*) and yellow scale (*A. citrina*). *Ablerus clisiocampae* were associated with pupal *Aphytis aonidiae* and pupal and pharate adult *C. bifasciata*. All *Ablerus clisiocampae* reared for this study were females.

Key Words: *Ablerus clisiocampae, Aphytis aonidiae, Comperiella bifasciata,* hyperparasitism, parasitoids, *Quadraspidiotus perniciosus,* San Jose scale, *Aonidiella aurantii,* California red scale, *Aonidiella citrina,* yellow scale

The aphelinid parasitoid *Ablerus clisiocampae* Ashmead has been reared both from lepidopteran eggs and diaspidid scale insect hosts (Darling and Johnson 1984, Polaszek 1991). There has been confusion, however, regarding the exact host relationships exhibited by this species. The genus *Ablerus* has historically been considered largely or exclusively hyperparasitic (Viggiani 1984, 1990), and some authors have assumed that *A. clisiocampae* attacks primary parasitoids of the hosts from which it has been reared (Muma 1959, Hughes 1960, Viggiani 1981). Also, Ehler (1995) found that *A. clisiocampae* was the smallest of a guild of parasitoids associated with obscure scale, *Melanaspis obscura* (Comstock) (Homoptera: Diaspididae), and that its phenology was consistent with a hyperparasitic life history. Although these lines of reasoning are consistent with hyperparasitism, the information required to distinguish between primary and secondary parasitism in this species has not been available to date. Here, we provide direct evidence that *A. clisiocampae* hyperparasitizes primary parasitoids of three armored scale insects (Homoptera: Diaspididae): the San Jose scale, *Quadraspidiotus perniciosus* (Comstock); the California red scale, *Aonidiella aurantii* (Maskell); and the yellow scale, *A. citrina* (Coquillet).

San Jose Scale System

San Jose scale is a pest of fruit, nut, and ornamental trees. Its most important natural enemy in California is the parasitoid *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae) (Gulmahamad and DeBach 1978a, Heimpel et al. 1996). *Aphytis aonidiae* lays eggs singly on the external surface of the scale insect under the scale cover, and larvae and pupae develop ectoparasitically (Gulmahamad and DeBach 1978b, Heimpel et al. 1996). We encountered *Ablerus clisiocampae* underneath San Jose scale covers during a study aimed at quantifying parasitism of San Jose scale by *A. aonidiae* on almonds.

We collected 20-cm twig samples from a 4 ha section of an organically managed almond orchard in Sutter County, California, that supported a moderate infestation of San Jose scale (Heimpel et al. 1996). Samples were taken to the laboratory, and scale insects were individually examined at 40×. Each scale insect was noted as being healthy, dead from unknown causes, or parasitized, and the identity and stage of each parasitoid was recorded.

Samples were taken during 1992, 1993 and 1994. Between August and October 1994, we recovered twelve specimens of *Ablerus clisiocampae,* all of which were female. These individuals were discovered as larvae (n = 9) or pupae (n = 3) and reared to adulthood in glass vials. Two of the 9 larvae were observed feeding ectoparasitically on *Aphytis aonidiae* pupae, providing direct evidence of hyperparasitism (Fig. 1a). In both of these cases, remains of the scale insect and the *A. aonidiae* pupa were clearly visible underneath the scale cover. We did not find *A. aonidiae* or scale insect remains associated with the other 10 *Ablerus clisiocampae.* We were unable to classify these cases as either primary or secondary parasitism, and suspect that scale insect and/or *Aphytis* remains were lost during handling of the samples. Scale insects associated with *Ablerus clisiocampae* represented a small fraction of the total number sampled. Between August and October of 1994, we examined 1,462 adult female scale insects, 19.7% of which were parasitized by *Aphytis aonidiae* (GEH and JAR, unpublished data).

California Red Scale and Yellow Scale System

The California red scale (CRS) and yellow scale are important pests of citrus worldwide, including California. *Comperiella bifasciata* Howard (Hymenoptera: Encyrtidae) is a solitary parasitoid of both CRS and the yellow scale, although it is generally considered to be of secondary importance to *Aphytis melinus* DeBach as a control agent in many citrus growing regions (Flaherty et al. 1973, Blumberg and Luck 1990). *Comperiella bifasciata* is an endoparasitoid, laying one or a few eggs inside the bodies of armored scales (Rosenheim and Hongkham 1996). At most, only one egg survives to adulthood, and many eggs become encapsulated by the host (Blumberg and Luck 1990, Ode and Rosenheim 1998). In a study examining host encapsulation rates in the field, we encountered *Ablerus clisiocampae* along with the remains of *C. bifasciata* pupae and pharate adults that had parasitized both CRS and yellow scale (PJO, unpublished data).

Leaf samples infested with both species of armored scale were collected weekly from an organic mandarin orange grove in Glenn County, California, between June and October 1995. Scales were examined under a dissecting microscope at 40× and their condition was scored as described above for the San Jose scale. When *A. clisiocampae* individuals were found, they were always in association with the remains of *C. bifasciata.* Overall, 2,391 female CRS and yellow scales were examined, 875 of which were parasitized by *C. bifasciata,* and approximately 400 of which were parasitized by *Aphytis* (probably *A. melinus*). *Ablerus clisiocampae* was found to have hyperparasitized *C. bifasciata* in 213 cases;

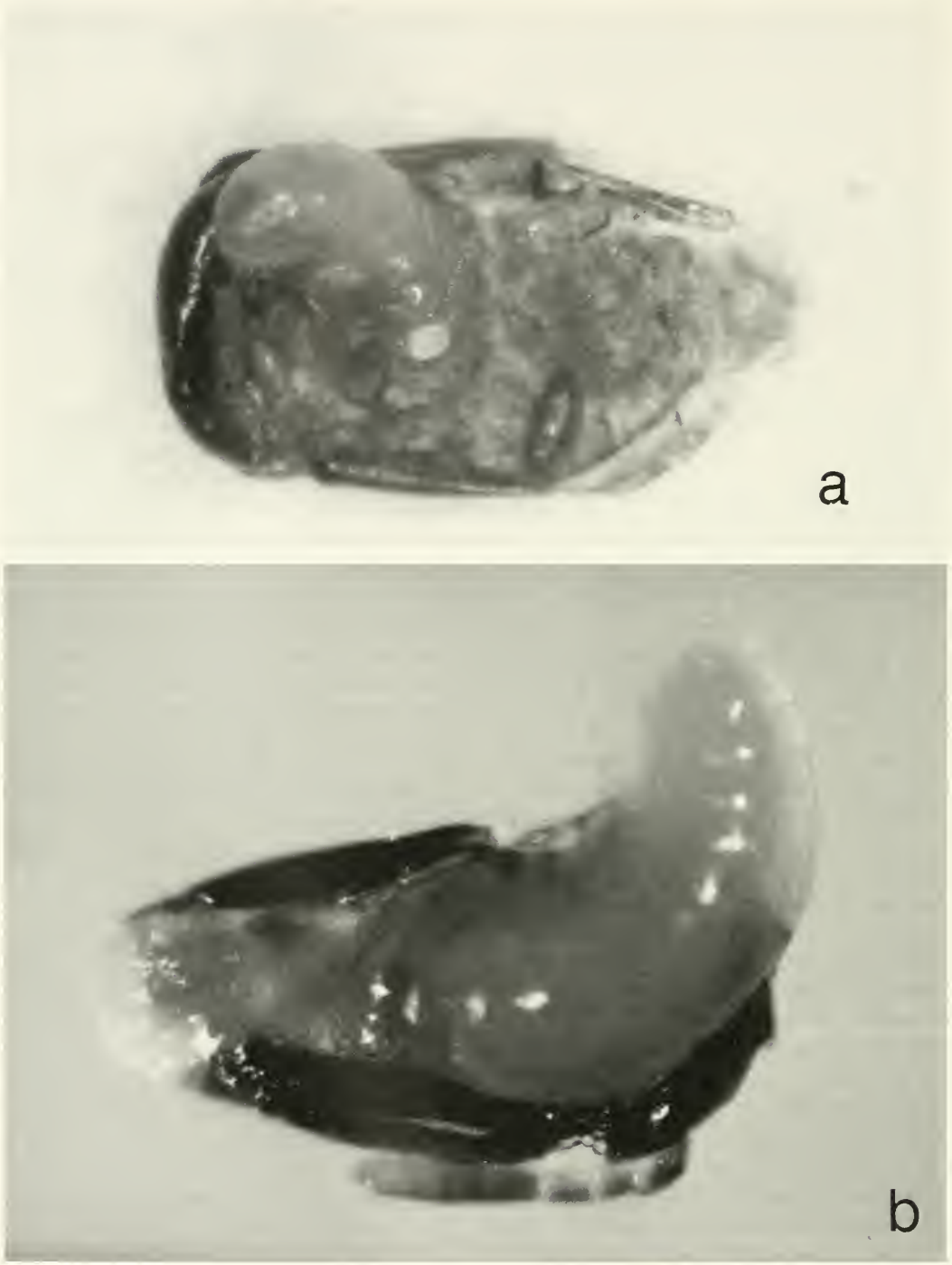

Fig. 1. *Ablerus clisiocampae*. a, Larva feeding on *Aphytis aonidiae* pupa. b, Larva feeding on a female *Comperiella bifasciata* pharate adult.

in 27 of these cases, we clearly saw an *A. clisiocampae* larva feeding ectoparastically on *C. bifasciata* pharate adults (Fig. 1b; PJO, unpublished data). We successfully reared these individuals to adulthood, and all *A. clisiocampae* were females. Voucher specimens of *A. clisiocampae* reared from San Jose scale, CRS and yellow scale have been deposited at the Bohart Insect Museum, University of California, Davis.

Discussion

Our rearing data and dissections of armored scales with developing parasitoids demonstrate that *A. clisiocampae* develops as an obligate hyperparasitoid. *Ablerus clisiocampae* was observed feeding on the pupae or pharate adults of ectoparasitic and endoparasitic primary parasitoids, and no primary parasitism was observed despite extensive sampling of primary host material.

All of the *Ablerus clisiocampae* individuals that we reared were females. Although female-biased sex ratios are known in this species (Smith and Goyer 1985, Ehler 1995), a complete lack of males has not been reported. An all-female sex ratio in our samples could be explained in at least two ways. First, the populations could be thelytokous. Although thelytoky has not been reported in this species, it is known from a number of chalcidoid species, including aphelinids (Werren 1997). In most of these species, thelytoky is linked to the presence of parthenogenesis-inducing endosymbionts, and can be present in some populations and absent in others (e.g., Stouthamer and Kazmer 1994). Alternatively, the populations of *A. clisiocampae* that we encountered may be heterotrophic, with the males feeding on a non-sampled host. Various forms of heterotrophism are found in the Aphelinidae (Walter 1983), but no evidence for such behavior exists for *A. clisiocampae* because both sexes have been reared from Lepidoptera (Darling and Johnson 1984, Smith and Goyer 1985) and Homoptera (Pinto 1980, Ehler 1995).

Acknowledgments

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KEY TO SELECTED PYRALOIDEA (LEPIDOPTERA) LARVAE INTERCEPTED AT U.S. PORTS OF ENTRY: REVISION OF PYRALOIDEA IN "KEYS TO SOME FREQUENTLY INTERCEPTED LEPIDOPTEROUS LARVAE" BY D. M. WEISMAN 1986

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Abstract.—A key to frequently intercepted lepidopterous larvae, designed for U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA, APHIS) identifiers at U.S. ports, was last revised in 1986. Since then many changes have occurred in the classification, nomenclature, and the nature of commodities being imported into the U.S. In this revision of the section on Pyraloidea, species recently intercepted are included, the most recent generic combinations are used, and families and subfamilies are now included in the key. Distributions are updated, stating if the species occurs in Hawaii or restricted areas of the continental United States. A "Note" section explains changes and additions, and gives references to further information. Two tables are provided, one to the classification of Pyraloidea with reference to placement in the key and another to the hosts and/or commodities.

Key Words: continental United States, Florida, Hawaii, hosts, Pyralidae, Crambidae

The Pyraloidea is estimated to be the second largest superfamily in the Lepidoptera, with more than 16,000 described species worldwide. Pyraloid caterpillars are very diverse in what they eat: "they consume dried or decaying plant or animal matter, wax in bee and wasp nests, and living plants. Some are known to be inquilines in ant nests (some Galleriinae), predators of scale insects (some Phycitinae), and aquatic scavengers in flowing water (some Nymphulinae) (Solis 1997). The plant feeders can be leaf rollers, leaf tiers, leafminers, and stem borers, and sometimes a combination. Pyraloid caterpillars are pests that cause damage and economically affect crops such as rice, sugarcane, corn, tomatoes, and many more; some are worldwide pests of stored products such as grains and fruits (Solis 1996).

Because so many pyraloid caterpillars are intercepted at ports in commodities being imported into the United States, the Pyraloidea part of "Keys for the identification of some lepidopterous larvae frequently intercepted at quarantine" by Hahn W. Capps, Division of Insect Identification, Bureau of Entomology and Plant Quarantine, U.S. Department of Agriculture was first published in 1939. It was published again in Spanish (Capps 1955) by the Agriculture Department of Mexico and again in English (Capps 1956, 1963) with only nomenclatural revision. It was not significantly revised again until 1986, when D. M. Weisman published "Keys for the identification of some frequently intercepted lepidopterous larvae." He added 40 species and replaced the Heinrich (1916) system of setal

nomenclature with the Hinton (1946) system. The revision presented here adds new taxa, incorporates recent new combinations, and provides keys to the family and subfamily levels of Pyraloidea. This revision also updates distributions, stating if taxa occur in restricted areas of the continental U.S. and Hawaii. A "Note" section explains changes and additions, adds relevant information, and gives references to further information. Two tables provide host and classification information.

The Pyraloidea has undergone both phylogenetic and nomenclatural changes because it is a group where taxonomists are actively pursuing questions that have both theoretical and applied ramifications. In the 1980's, Minet published a series of morphological papers on the tympanal organs in the Lepidoptera, including the Pyraloidea (1982). Based on the morphologically distinct tympanal organs and the work on larvae by Hasenfuss (1960), Minet proposed elevating two groups, known in the informal sense as Pyraliformes and Crambiformes (Munroe 1972), to Pyralidae and Crambidae. Most workers in the Pyraloidea agree with Minet (e.g., Munroe 1989, Solis and Mitter 1992). Taxonomy is not a static field but a field where new morphological and biological information continually becomes available, and it is necessary to change the classification to reflect this new information. In addition, several major checklists (Munroe et al. 1995, Shaffer et al. 1996) from several major geographic areas have been published in the last ten years with many new combinations and synonymies. Table 1 gives the current classification of Pyraloidea as an alphabetical list of the taxa treated in this work in the two families by subfamily, with the number of the couplet where they are found in the key for quick retrieval.

Description of the Key and Its Components

Capps' (1939) description of the function and basis of his key is still applicable today: "The following keys are intended to assist quarantine inspectors in recognizing the lepidopterous larvae most frequently intercepted at ports of entry and are based on the differential characters noted in the literature, and on the larval collection and host catalogue in the United States National Museum." The title of this revision reflects a change from "most frequently" taxa intercepted to "selected" taxa intercepted. I retained all taxa included in Weisman's key even though the species may no longer be intercepted frequently; this is in part because the species intercepted depend on the commodities being imported into the U.S. and these species may again be intercepted in the future. The addition of species to this current key is based on the actual interceptions submitted by APHIS port identifiers. Specimens are submitted for identification until the port identifier receives "port authority" for the identification of particular species; with this authority, they no longer send specimens for verification of that species. The top twelve species sent to the SEL (Systematic Entomology Laboratory) for identification in order from more frequent to less frequent during 1998 are: *Ectomyelois ceratoniae, Cadra cautella, Leucinodes orbonalis, Diatraea considerata, Spoladea recurvalis, Neoleucinodes elegantalis, Etiella zinckenella, Congethes* sp., *Pyrausta* sp., *Phidotricha erigens, Plodia interpunctella.*

Capps (1939) also wrote: "In using the keys, it should be borne in mind that their validity is dependent on three factors, viz., (1) structure, (2) origin, and (3) host." The origin referred to by Capps indicates the country where the commodity supposedly originated and does not imply evolutionary origin; for this reason Weisman (1986) probably chose to use the term "distribution" rather than "origin." The origin documented by port identifiers is the origin of the vehicle transporting the commodity prior to entering the U.S. The point of origin of the insect could be several ports removed if the vehicle made multiple stops, or en-

Table 1. Classification of Pyraloidea (number refers to couplet in the key).

PYRALOIDEA
CRAMBIDAE
CRAMBINAE
Chilo suppressalis (Walker) – 31
Diatrea sp. – 31
Eoreuma loftini (Dyar) – 30
EVERGESTINAE
Evergestis rimosalis (Guenée) – 37
GLAPHYRIINAE
Hellula rogatalis (Hulst) – 39
Hellula phidilealis (Walker) – 39
NYMPHULINAE
Parapoynx diminutalis Snellen – 27
PYRAUSTINAE
Achyra rantalis (Guenée) – 41
Ostrinia nubilalis (Hübner) – 36
Pyrausta sp. – 33
SPILOMELINI (or SPILOMELINAE)
Conogethes spp. – 34
Diaphania nitidalis (Stoll) – 49
Diaphania indica complex – 49
Hendecasis duplifascialis Hampson – 47
Herpetogramma bipunctalis (Fabricius) – 43
Leucinodes orbonalis (Guenée) – 50
Lineodes integra (Zeller) – 46
Loxomorpha flavidissimalis Grote – 41
Maruca vitrata (Fabricius) – 35
Megastes sp. – 35
Neoleucinodes elegantalis (Guenée) – 50
Rhectocraspeda periusalis (Walker) – 43
Spoladea recurvalis Fabricius – 45
Udea rubigalis (Guenée) – 46
SCHOENOBIINAE – 28
PYRALIDAE – 1
CHRYSAUGINAE – 22
EPIPASCHIINAE
Phidotricha erigens (Ragonot) – 19
GALLERIINAE
Alpheias conspirata Heinrich – 24
Corcyra cephalonica (Stainton) – 26
Paralipsa gularis (Zeller) – 26
Genopaschia protomis Dyar – 24
Trachylepidia fructicassiella Ragonot – 25
PHYCITINAE
Amyelois transtilla (Walker) – 13
Ancylostomia stercorea (Zeller) – 8
Cadra cautella (Walker) – 17
Cadra figulilella (Gregson) – 18
Cadra calidella (Guenée) – 18
Cryptoblabes sp. – 6
Ectomyelois ceratoniae (Zeller) – 13
Elasmopalpus lignosellus (Zeller) – 6
Ephestia elutella (Hübner) – 16
Ephestia kuehniella (Zeller) – 16
Etiella zinckenella (Treitschke) – 20
Fundella pellucens Zeller – 10
Homoeosoma electellum Hulst – 11
Hypsipyla sp. – 9
Moodna bisinuella Hampson – 9
Mussidia nigrivenella Ragonot – 4
Plodia interpunctella (Hübner) – 14
PYRALINAE
Pyralis farinalis Linnaeus – 21
Aglossa caprealis (Hübner) – 21

tirely outside the vehicle's itinerary if infested cargo was transferred en route.

Further, Capps (1939) wrote: "Moreover, the characters used for separating the families are not completely diagnostic for the entire family but will serve to separate the species treated here." This is emphasized for two reasons: one, the percentage of lepidopterous larvae known is very small, usually only the larval morphology of the pest species in a genus is well known, and hence, the distribution of the characters across taxa are unknown; and two, the loss or reduction of characters in larvae in general is inferred to occur extensively (see also Passoa 1985).

All current taxonomic and phylogenetic information has been incorporated into the revision of this key. Distributions vary according to the information provided with the submitted material and are based specifically on the usage by port identifiers; for example, a country versus an area of a continent. It is stated if the species occurs in Hawaii or a few states in the continental U.S. Changes in distribution in this revision are based on the current literature and unpublished localities in the Pyraloidea collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. New records in the U.S. are taken into account if there is evidence to support that a population has been established. It is common in certain parts of the U.S. adjoining the Gulf of Mexico to catch one or more adult(s) of a species at light, but this is not

evidence that the species is established in the U.S. Specifically, distribution records from Hawaii are from Nishida (1992). He uses three words to reflect residency status: endemic, indigenous, and adventive. I use only adventive when applicable: "immigrant" is used in place of "introduced" to differentiate from those that were purposely introduced. Species that are known only from quarantine records (reported as intercepted) or those considered not established are present in the database, but do not appear in the checklist (Nishida 1992). The "Old World" includes all land masses except the Western Hemisphere.

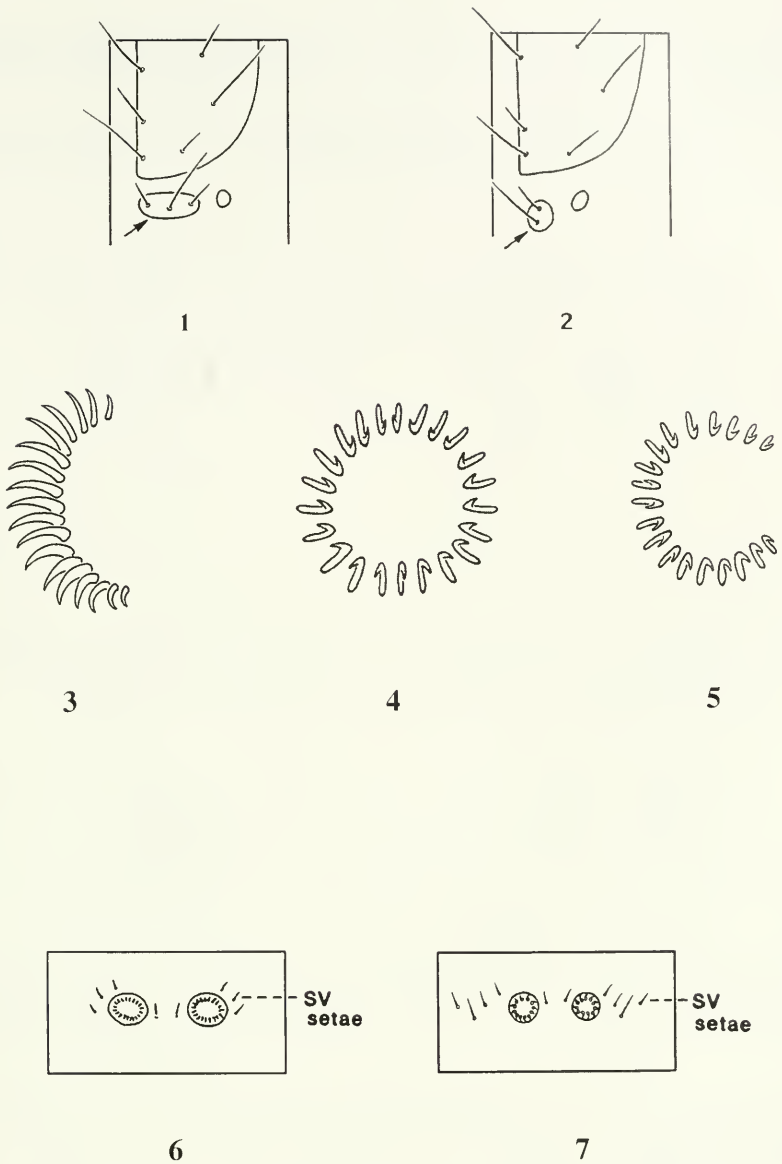
The plant names are based primarily on the names given to commodities being imported or brought into the U.S. for any variety of purposes; in this work the biological term "host" and the economic term "commodity" are often one and the same. The names of hosts are either a scientific name or a common name as supplied by port identifiers and checked against Brako, Rossman, and Farr (1995) for U.S. names, and Mabberley (1997) for all other localities and are listed under the "Hosts" section of each species. In the key, the 1998 host records are directly from the SELIS database (Systematic Entomology Laboratory Identification Service) as submitted by port identifiers and listed alphabetically. Pre-1998 records can be from a variety of sources and are primarily those listed in Weisman (1986), with additions from the SELIS database, the USNM larval collection, and are mainly historical records. If the scientific name of a host appeared in both the 1998 list and pre-1998 list, it was removed from the pre-1998 list. The lists of hosts at times lack detail (e.g., "stored vegetable products") because many pyraloid pest species are highly polyphagous. Table 2 gives the hosts of the pyraloid larvae. If a scientific name for the commodity is given, the table refers to the common name as given by the port identifiers also; scientific names were not generally used prior to the mid-1980's. The common name is followed by the scientific name in brackets for purposes of cross-indexing.

The "Note" sections comment on a variety of topics that may be useful to the port identifier, it is not meant to be comprehensive: on character variability, explanations of recent nomenclatural changes, nomenclatural method of reporting based on morphological and distributional information available, and relevant literature. The amount of literature available is scattered and very large for pest species, and is less large for geographical works (e.g., Carter 1984, Mutuura et al. 1965). This work does not attempt to review the entirety of the literature, but rather to point to seminal literature that provides relevant information.

How to Distinguish Pyraloidea Larvae

Pyraloidea larvae can be distinguished from other Lepidoptera larvae by a combination of characters. Many "micro" lepidopteran groups have 3 setae in the prespiracular group of the prothorax (Fig. 1), but some may have 2 or 1 (Stehr 1987) and they do not have typical pyraloid crochets (see below). Pyraloids, noctuids, and other "macro" lepidopteran groups have two setae in the prespiracular group of the prothorax (Fig. 2) (Stehr 1987). The Noctuoidea and Carposinidae, two groups that are intercepted frequently and are of importance to port identifiers, can be confused with pyraloids by the presence of two setae in the prothoracic prespiracular group. But pyraloids can be distinguished from noctuoids because noctuoids have the crochets in a mesoseries (Fig. 3), and pyraloids have the crochets in a complete circle or penellipse (Figs. 4–5).

Larvae of the Carposinidae are also confused with pyraloids because they also have two setae in the prespiracular group of the prothorax and crochets in a complete circle. Generally, pyraloids can be separated from carposinids because pyraloids have 3 subventral setae on abdominal segments 3 to 6 (Fig. 6), and carposinids usually have 4 subventral setae (Fig. 7), but the number of



Figs. 1–7. Characters to distinguish larvae of Pyraloidea (see text). 1–2, Prespiracular group of setae of prothorax (arrows). 3, Crochets in a mesoseries. 4, Crochets in a complete circle. 5, Crochets in a penellipse. 6–7, Subventral (SV) setae on abdominal segment.

subventral setae may vary from segment to segment (see Common 1990). It should be noted here that Weisman (1986) used "the spiracle on abdominal segment 8 well above level of those on preceding segments" to separate them from pyraloids, but many pyraloids have the spiracle on segment 8 above the level of those on the preceding segments.

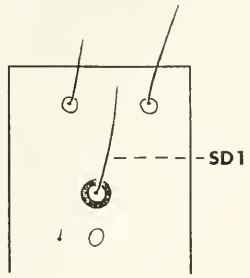
For recent, more general information on other Nearctic pyraloid larvae and lepidopterous larvae and comparisons to other families and other geographic regions see Stehr (1987) and Common (1990).

Key to Selected Intercepted Pyraloidea Larvae

1. Sclerotized ring around seta SD1 on A8 (missing in a some phycitines) (Fig. 8); three (sometimes two) setae in the L group on A9 (Fig. 9) . . . . . **Pyralidae** 2

Subfamilies: Chrysauginae, Epipaschiinae, Galleriinae, Phycitinae, Pyralinae

Note: Sclerotized rings sometimes hard to see and appear as shiny, unsclerotized rings; 2 L setae in *Etiella zinckenella* (Tr.) and others



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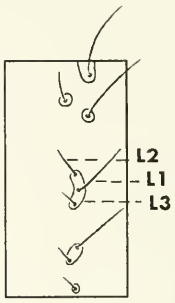
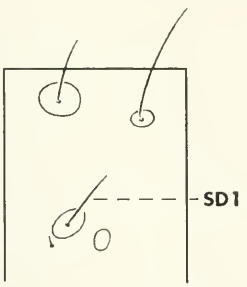


9

– No sclerotized ring around seta SD1 on A8 (Fig. 10); one seta in the L group on A9 (Fig. 11) . . . . . **Crambidae** 27

Subfamilies: Cathariinae, Crambinae, Cybalomiinae, Evergestinae, Glaphyriinae (includes Dichogaminae), Linostinae, Midilinae, Musotiminae, Noordinae, Nymphulinae, Odontiinae, Pyraustinae (includes Spilomelinae), Schoenobiinae, Scopariinae, Wurthiinae



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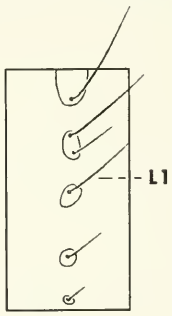
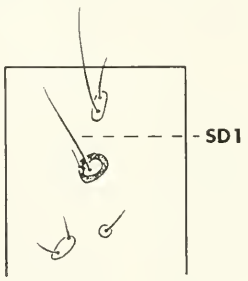


11

2. Sclerotized ring around seta SD1 on mesothorax, metathorax, or A1 (Fig. 12) . . . . . **Galleriinae, Chrysauginae, Phycitinae** 3

Note: Sclerotized ring sometimes absent on these segments, but in taxa not covered in this key (Solis and Mitter 1992)



12

– No sclerotized ring around seta SD1 on mesothorax, metathorax, or A1 . . . . . **Pyralinae, Epipaschiinae, few Phycitinae** 19

3. Sclerotized ring around seta SD1 of metathorax or A1 . . . . . **Chrysauginae, Galleriinae** 22
– Sclerotized ring around seta SD1 on mesothorax . . . . . **most Phycitinae** 4

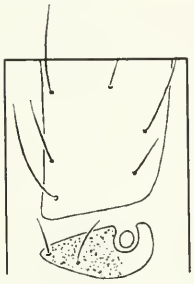
4. Sclerotized ring around seta SD1 on A2 to A7 . . . . . ***Mussidia nigrivenella*** Ragonot

Distribution: west tropical Africa; does not occur in the U.S.
Hosts: 1998: stored seeds
pre-1998: butter beans, cacao, calabar beans, carob or locust bean, stored grains (cereals)
Note: see Aitken 1963, Corbet and Tams 1943

– Sclerotized ring around seta SD1 of mesothorax . . . . . **other Phycitinae** 5

Note: see Hinton 1943; some Phycitinae lack this character, e.g., *Etiella* sp.

5. Prespiracular shield of prothorax extending below and behind the spiracle (Fig. 13) or completely enclosing spiracle (Fig. 16) 6
– Prespiracular shield of prothorax never extending below and behind spiracle (Fig. 14) 7



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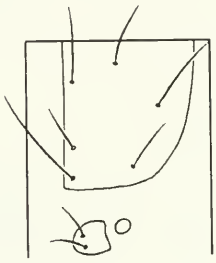
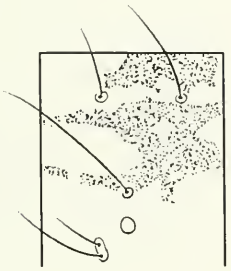


14

6. Posterior portion of prespiracular shield weakly pigmented (Fig. 13); body pink with whitish discontinuous longitudinal bands on most segments (Fig. 15); ring around mesothoracic seta SD1 not prominently sclerotized (Fig. 12) . . . . . ***Elasmopalpus lignosellus*** (Zeller)

Distribution: Western Hemisphere; adventive in Hawaii
Hosts: 1998: *Ananas comosus, Asparagus officinalis, Coffea arabica, Corylus avellana, Maranta* sp., *Mentha* sp., *Mimosa pigra, Sida* sp., *Sorghum* sp., *Zea mays* (unpopped corn)
pre-1998: alfalfa, beans, cow peas, Johnson grass, peas, soybeans, strawberries, string beans, sugarcane
Note: see Heinrich 1956, Luginbill and Ainslie 1917, Neunzig 1979



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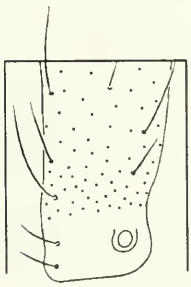

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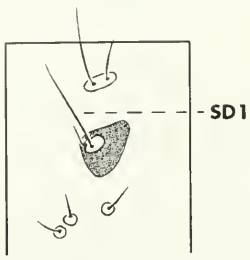
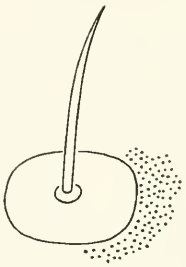


17

– Prespiracular shield completely enclosing spiracle weakly pigmented (Fig. 16); prominent longitudinal dark bands on all segments; ring around mesothoracic seta SD1 prominently sclerotized (Fig. 17) . . . . . ***Cryptoblabes* sp.**

Distribution: Europe, Africa, Asia
Hosts: 1998: *Citrus sinensis, Dimocarpus longan, Musa* sp., *Phoenix* sp., *Psidium guajava, Punica granatum*
pre-1998: *Amaranthus* sp., *Chaenomeles japonica,* grapes, *Lythrum* sp., pineapple, raisins, *Tamarix* sp.
Note: should be reported as "*Cryptoblabes gnidella* (Millière)" if the origin is from the Western Hemisphere where it was introduced (Heinrich 1956); does not occur in the continental U.S. or Hawaii; see Neunzig 1986

7. Integument granulose under low magnification (30×) (Fig. 18) 8

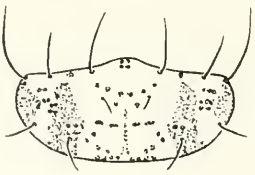


18

– Integument not granulose under low magnification 10

8. Prothoracic shield with black areas on lateral margins and longitudinal black areas on either side midway between center line and lateral margins (black areas on either side of center line may be very faint) (Fig. 19) . . . . . ***Ancylostomia stercorea*** (Zeller)

Distribution: tropical Western Hemisphere including southeastern U.S., Florida to Texas
Hosts: 1998: *Cajanus cajanus, Phaseolus vulgaris, Pisum sativum, Rumex* sp.
pre-1998: chickpeas, cow peas
Note: see Heinrich 1956



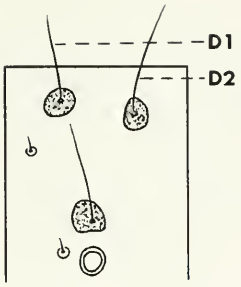
19

– Prothoracic shield not with the above color pattern 9

9. Pinacula of body setae large and dark (Fig. 20); seta D2 of A1 to A7 below level of seta D1 (Fig. 20) . . . . . ***Hypsipyla* sp.**

Distribution: tropical Western Hemisphere including southern Florida

Hosts: 1998: *Zea mays* (unpopped corn)
pre-1998: crabwood, mahogany, Spanish cedar logs
Note: see Heinrich 1956, Neunzig 1990



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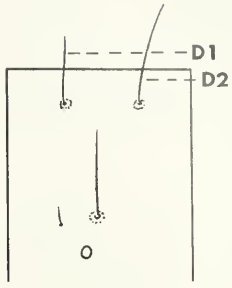


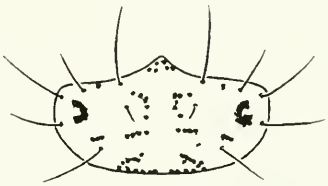
21

– Pinacula of body setae very small and pale (Fig. 21); seta D2 of A1 to A7 at level of seta D1 (Fig. 21) . . . . . ***Moodna bisinuella*** Hampson

Distribution: southern Texas to Mexico, El Salvador
Hosts: *Zea mays*
Note: see Heinrich 1956, Neunzig 1990

10. Prothoracic shield yellow with pattern of dark marks as illustrated (Fig. 22) . . ***Fundella pellucens*** Zeller

Distribution: tropical Western Hemisphere including Florida
Hosts: 1998: *Cajanus cajun*
pre-1998: beans, cow peas, lima beans, peas
Note: see Heinrich 1956

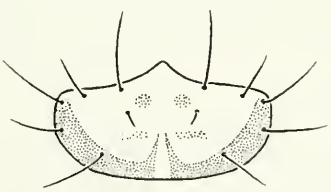


22

– Prothoracic shield yellowish without the pattern as above 11

11. Prothoracic shield with black areas on lateral and posterior margins (sometimes without black area on posterior margin) (Fig. 23); prominent longitudinal dark bands on all segments (Fig. 24); head with dark band from ocelli to posterior margin . . . . . ***Homoeosoma electellum*** Hulst

Distribution: North and South America
Hosts: 1998: *Bidens* sp., *Helianthus annuus*
pre-1998: Asteraceae, cotton, oranges
Note: see Heinrich 1956, Neunzig 1997



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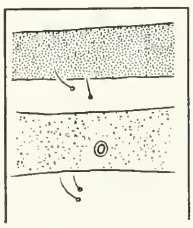
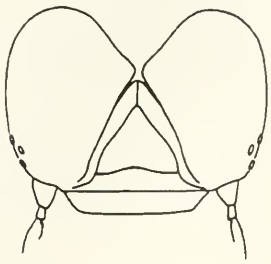


24

– Prothoracic shield yellowish without the pattern as in Fig. 23 12

12. Coronal suture absent (Fig. 25); A1 to A7 with a crescent-shaped patch above seta SD1 (usually reduced to a small smudge or missing in *Amyelois transitella*) (Fig. 26) 13



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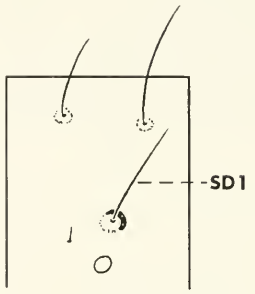
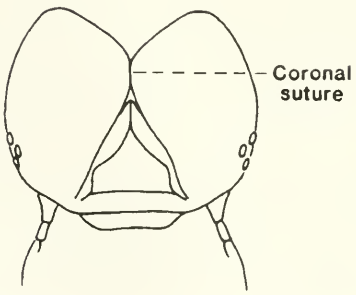


26

– Coronal suture present (Fig. 27); A1 to A7 without crescent-shaped patch above seta SD1 (Fig. 28) 14



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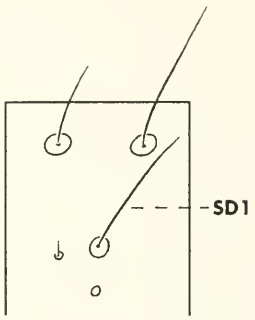
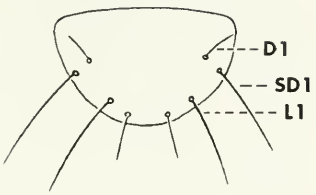


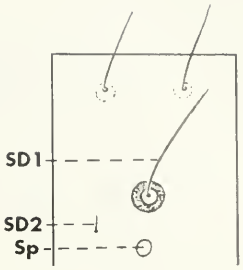
28

13. Anal plate with seta SD1 closer to seta D1 than to seta L1 (Fig. 29); seta SD2 of A8 usually separated from the spiracle by 2 or more times the diameter of the spiracle (Fig. 30); sclerotized ring around seta SD1 on A8 usually complete (Fig. 30) . . . . . ***Ectomyelois ceratoniae*** (Zeller)

Distribution: nearly cosmopolitan including Florida
Hosts: 1998: *Annona* sp., *Capsicum* sp., *Castanea sativa, Cereus* sp., *Chimonanthus* sp., *Cucurbita* sp., *Cydonia oblonga, Ficus carica, Juglans nigra, Lansium domesticum, Malus sylvestris, Mangifera indica, Phaseolus* sp., *Phoenix dactylifera, Pithecellobium dulce, Prunus avium, Psidium guajava, Pyrus communis, Pyrus pyriflora, Punica granatum, Sesbania* sp., *Tamarindus indica, Zea mays*
pre-1998: carob or locust bean, dates, legumes, nuts, and others
Note: If the origin is from the tropical areas of the Western Hemisphere it should be reported as "probably *E. decolor*"; see Neunzig 1979, 1990



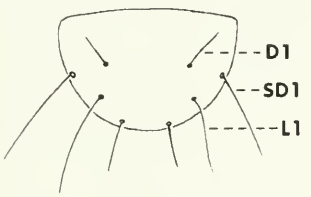
29



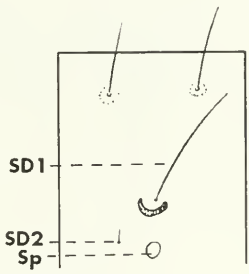
30

– Anal plate with seta SD1 equidistant from setae D1 and L1 (Fig. 31); seta SD2 of A8 usually separated from the spiracle by one to 1.5 times the diameter of the spiracle (Fig. 32); sclerotized ring around seta SD1 on A8 incomplete (Fig. 32) . . . . . ***Amyelois transtilla*** (Walker)

Distribution: tropical Western Hemisphere including southern U.S.
Hosts: 1998: none
pre-1998: *Annona* sp., *Caesalpinia pulcherrima, Cajanus cajan, Citrus sinensis, Cydonia oblonga, Juglans* sp., *Malus* sp., *Malus sylvestris, Mangifera indica,* peach, peony, *Punica granatum, Pyrus communis, Randia* sp., *Tamarindus indica, Zea mays,* and other fruits and pods
Note: see Neunzig 1990



31

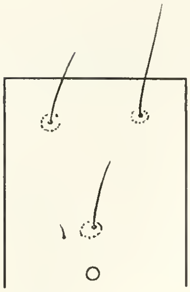


32

14. A1 to A8 apparently without pinacula (pinacula concolorous with body and not evident) (Fig. 33) . . . . . ***Plodia interpunctella*** (Hübner)

Distribution: cosmopolitan, adventive in Hawaii
Hosts: 1998: *Berberis* sp., *Camellia sinensis, Capsicum* sp., *Capsicum annuum, Castanea sativa, Cicer arietinum, Ficus carica, Gleditsia* sp., *Morus* sp., *Oryza* sp., *Phaseolus* sp., *Pistacia* sp., Poaceae, *Prosopis* sp., *Prunus avium, Prunus domestica, Prunus persica, Punica granatum, Vicia faba, Vitis* sp., *Ziziphus jujuba*
pre-1998: stored fruit, grain, and vegetable products
Note: see Neunzig 1990

– A1 to A8 with small pigmented pinacula (Fig. 34) 15



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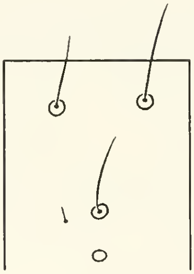
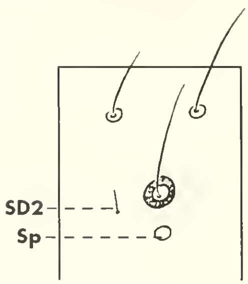
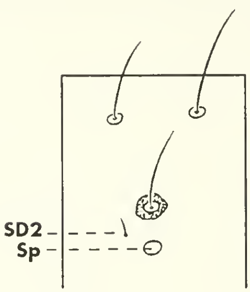


34

15. A8 with seta SD2 separated from spiracle by 2 to 3 times the horizontal diameter of the spiracle (Fig. 35) 16
– A8 with seta SD2 separated from spiracle by a distance equal to the horizontal diameter of the spiracle (Fig. 36) 17



35



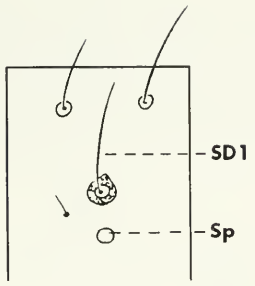
36

16. Spiracle of A8 as large as the area enclosed by the sclerotized ring around seta SD1 (Fig. 37) . . . . . . ***Ephestia kuehniella*** (Zeller)

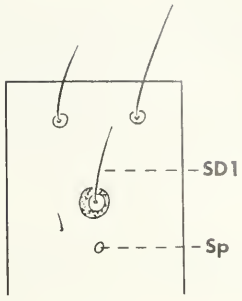
Distribution: nearly cosmopolitan; does not occur in Hawaii
Hosts: 1998: *Annona* sp., *Dennettia* sp., *Chrysophyllum* sp., *Moringa oleifera*
pre-1998: stored grain, stored and dried vegetable products
Note: see Neunzig 1990

– Spiracle of A8 two-thirds or less as broad as the area enclosed by the sclerotized ring around seta SD1 (Fig. 38) . . . . . . ***Ephestia elutella*** (Hübner)

Distribution: Nearly cosmopolitan; does not occur in Hawaii
Hosts: 1998: *Acanthocereus sp., Allium sp., Brassica sp., Capsicum sp., Castanea sp.,* cereal products, *Juglans nigra, Medicago sativa, Oryza sativa, Protea sp., Prunus sp., Prunus avium, Punica granatum, Vitis sp.*
pre-1998: stored and dried vegetable products
Note: see Neunzig 1990; early instars with partial sclerotization of SD1 ring A1 to A7



37

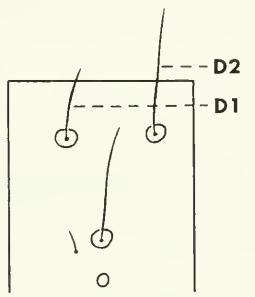


38

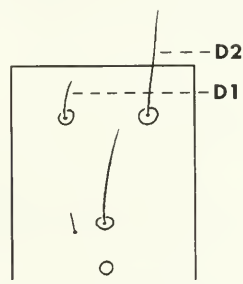
17. Seta D2 of A1 to A8, two to two and one-half times the length of seta D1 (Fig. 39) . . . . . ***Cadra cautella*** (Walker)

Distribution: cosmopolitan, adventive in Hawaii
Hosts: 1998: *Allium sativum, Anacardium* sp., *Ananas comosus, Arachis hypogaea, Areca* sp., *Bambusa* sp., *Berberis* sp., *Capsicum* sp., *Carica papaya, Citrus* sp., *Coffea arabica, Cucurbita* sp., *Guizotia abyssinica, Morus* sp., *Oryza sativa, Phaseolus* sp., *Phoenix dactylifera, Pisum sativum, Pithecellobium dulce, Prunus avium, Psidium guajava, Pyrus communis, Rosa* sp., *Rubus* sp., *Sesamum indicum, Tamarindus* sp., *Theobroma cacao, Vaccinium* sp., *Zea mays*
pre-1998: stored and dried vegetable products
Note: see Neunzig 1990

– Seta D2 of A1 to A8, three to five times the length of seta D1 (Fig. 40) 18



39



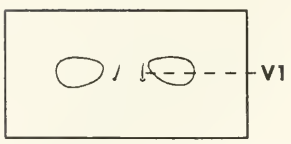
40

18. Metathorax with the distance between setae V1 2 times or less than the distance between seta V1 and the coxa (Fig. 41) . . . . . ***Cadra figulilella*** (Gregson)

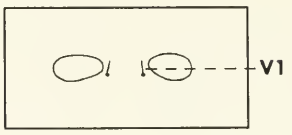
Distribution: nearly cosmopolitan; occurring in the continental U.S. and adventive in Hawaii
Hosts: 1998: *Allium sativum, Capsicum* sp., *Castanea sativa, Ficus* sp., *Ficus carica, Manihot esculenta, Morus* sp., *Phoenix dactylifera, Prunus* sp., *Prunus avium, Psidium guajava, Saccharum officinarum*
pre-1998: dried beans, fruits, nuts, and seeds
Note: see Neunzig 1990

– Metathorax with the distance between setae V1 3 to 5 times the distance between seta V1 and the coxa (Fig. 42) . . . . . ***Cadra calidella*** (Guenée)

Distribution: Mediterranean; does not occur in the U.S
Hosts: 1998: *Castanea* sp., *Ceratonia siliqua,* dried foodstuffs, *Ficus* sp., *Ficus carica, Morus* sp., *Phoenix* sp., *Prunus* sp.
pre-1998: dried fruit and nuts, *Plectranthus* sp. (seed), *Vitis vinifera*
Note: see Aitken 1963

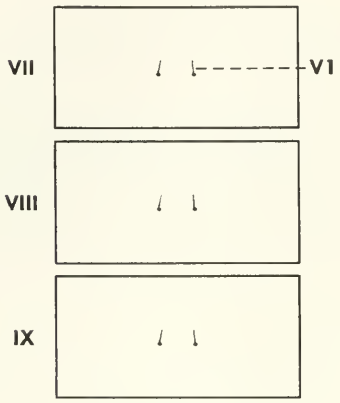


41

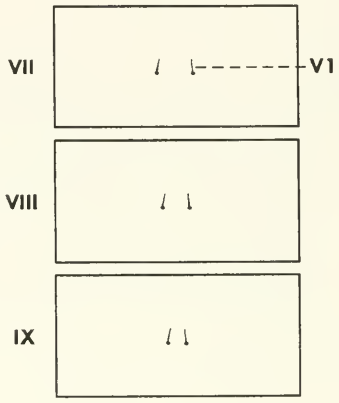


42

19. V1 on abdominal segment 7 as far apart as on segment 9 (Fig. 43); body without longitudinal dark bands . . . . . **Phycitinae, Pyralinae** 20



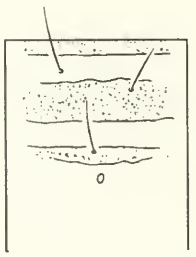
43



44

– V1 on abdominal segment 7 twice as far apart as on segment 9 (Fig. 44); body with longitudinal dark bands (Fig. 45) . . . . . **Epipaschiinae, *Phidotricha erigens*** (Ragonot)

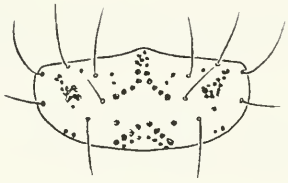
Distribution: tropical Western Hemisphere including southern Florida
Hosts: 1998: *Benincasa hispida, Mammea* sp., *Mimosa pigra, Petiveria alliacea, Zea mays, Zingiber* sp.
pre-1998: cotton, lima beans, loquats, mangos, sorghum, tamarinds
Note: misidentified in the literature as *Pococera atramentalis* Lederer (Solis 1993); see Allyson 1977



45

20. Prothoracic shield with pattern of dark markings as illustrated (Fig. 46); from the Western Hemisphere . . . . . **Phycitinae, *Etiella zinckenella*** (Treitschke)

Distribution: nearly cosmopolitan; does not occur in Hawaii
Hosts: 1998: *Cajanus cajan, Capsicum annuum, Castanea sativa, Cicer arietinum, Cucurbita* sp., *Cydonia oblonga, Lablab purpureus, Opuntia* sp., *Parkia* sp., *Phaseolus lunatus, Phaseolus vulgaris, Pisum sativum, Solanum tuberosum, Zea mays*
pre-1998: legumes and other stored vegetable products
Note: because several immatures of species are indistinguishable, it should be reported as "*Etiella* sp." if the origin is southeast Asia; markings on prothorax can be more or less distinct

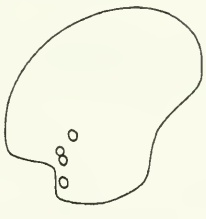


46

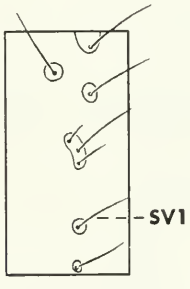
– Prothoracic shield not patterned as above 21

21. Head with only 4 distinct ocelli (ocelli I and II fused and ocellus VI usually missing) (Fig. 47); A9 with one subventral seta (Fig. 48) . . . . . ***Pyralis farinalis*** Linnaeus

Distribution: nearly cosmopolitan, does not occur in Hawaii
Hosts: 1998: *Allium sp.,* foodstuffs, *Narcissus tazetta,* packing
pre-1998: dried vegetable products
Note: the packing is usually associated with polished monuments, marble blocks, and tiles in wood crates



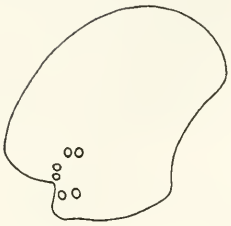
47



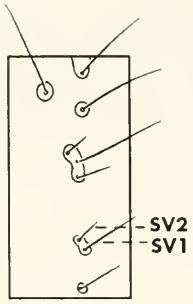
48

– Head with 6 ocelli (Fig. 49); A9 with two subventral setae (Fig. 50) . . . . . ***Aglossa caprealis*** (Hübner)

Distribution: Nearly cosmopolitan, does not occur in Hawaii
Hosts: 1998: *Allium sativum*
pre-1998: damp grain and rotting vegetable matter, *Nephelium lappaceum,* packing in crates, *Persea americana*

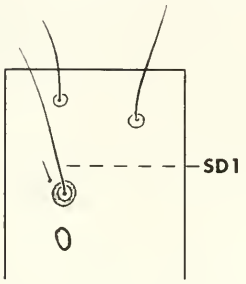


49

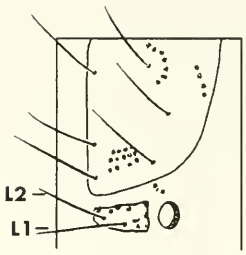


50

22. Sclerotized ring around seta SD1 of metathorax (Fig. 51) . . . . . **Chrysauginae**
– Sclerotized ring around seta SD1 of A1 (Fig. 51) . . . . . **Galleriinae** 23

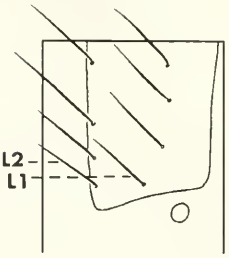


51

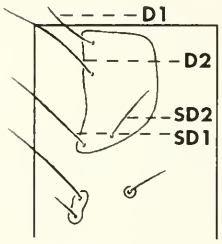


52

23. Prespiracular and prothoracic shields entirely fused (Fig. 53) 24
– Prespiracular and prothoracic shields not fused (Fig. 54) 25



53



54

24. Sclerotized rings around seta SD1 on A2 to A7 in addition to A1 and A8 . . . ***Alpheias conspirata*** Heinrich

Distribution: Mexico
Hosts: *Ananas comosus*

– No sclerotized rings around seta SD1 on A2 to A7; sclerotized rings around A1 and A8 only . . . . . ***Genopaschia protomis*** Dyar

Distribution: Panama
Hosts: *Ananas comosus*

25. Prespiracular shield of prothorax not extending below and behind spiracle (Fig. 52) 26
– Prespiracular shield of prothorax extending below and behind the spiracle (Fig. 55) . . . . . ***Trachylepidia fructicassiella*** Ragonot

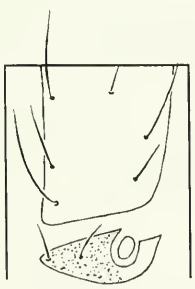
Distribution: pantropical
Hosts: 1998: *Cassia* sp., *Cassia fistula, Cassia grandis,* dried vegetable products, *Vigna* sp.
pre-1998: *Inga*

26. Sclerotized ring around seta SD1 on A1 and A8 not complete (Fig. 56); spiracular peritreme thicker on caudal margin (Fig. 56); pinacula of setae D1 and D2 on abdominal segments not pigmented (Fig. 56) . . . . . ***Corcyra cephalonica*** (Stainton)

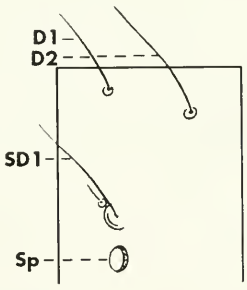
Distribution: cosmopolitan
Hosts: 1998: *Brassica* sp., *Guazuma ulmifolia, Lens* sp., *Oryza* sp., *Oryza sativa, Triticum* sp.
pre-1998: *Abelmoschus esculentus, Acacia* sp., *Arachis* sp., *Cassia* sp., cocoa beans, coffee, *Cola* sp., *Cuminum* sp., *Inga* sp., *Phaseolus vulgaris, Sesamum indicum, Sorghum* sp., stored vegetable products

– Sclerotized rings around seta SD1 on A1 and A8 complete (Fig. 57); spiracular peritremes of uniform thickness (Fig. 57); pinacula of setae D1 and D2 on abdominal segments pigmented (Fig. 57) . . . . . ***Paralipsa gularis*** (Zeller)

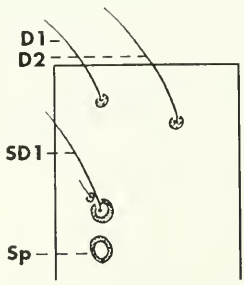
Distribution: nearly cosmopolitan, adventive in Hawaii
Hosts: 1998: *Capsicum annuum, Nephelium lappaceum, Phoenix dactylifera, Rhododendron* sp., *Zea mays*
pre-1998: *Ananas comosus, Areca catechu, Bambusa* sp., *Calophyllum brasiliense, Cassia* sp., *Castanea* sp., *Ceratonia siliqua,* dunnage, *Elasis* sp. *Lansium domestica, Oncidium* sp., papyrus, *Punica granatum, Solanum* sp., *Stirlingia* sp., stored vegetable products



55



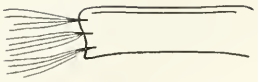
56



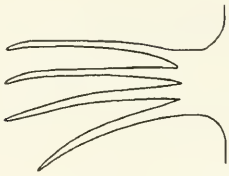
57

27. Lateral gills on body segments (Figs. 58, 59) . . . . . **Nymphulinae** . . . . . ***Parapoynx*** sp.

Distribution: southeastern Asia, Africa, Australia, Europe, U.S.
Hosts: 1998: *Hygrophila* sp., *Vallisneria* sp.
pre-1998: *Cabomba* sp., *Hydrilla* sp., *Limnophila* sp., *Myriophyllum* sp.
Note: Fig. 59 is an enlargement of one lateral gill, note base; *P. fluctuosalis* is adventive in Hawaii; see Goater 1986



58



59

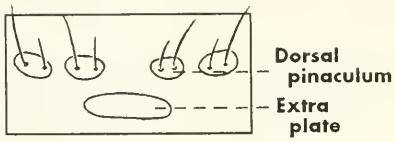
– Without lateral gills 28

28. With membranous sac or gibbosity anterior to prothoracic coxae . . . . . **Schoenobiinae**

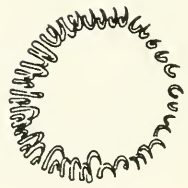
Hosts: 1998: *Typha latifolia*
pre-1998: *Pistia stratiotes*
Note: for further information on this group see Passoa (1987) and Stehr (1987)

– Without membranous sac or gibbosity anterior to prothoracic coxa 29

29. A single transverse plate posterior to dorsal pinacula on mesothorax (Fig. 60); crochets in complete circle (Fig. 61) . . . . . **Crambinae** 30



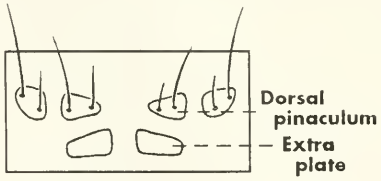
60



61

– A pair of transverse plates posterior to dorsal pinacula on mesothorax (Fig. 62) or plates absent; crochets in a mesal penellipse (Fig. 63) (or may be a circle weaker on lateral edge in *Lineodes integra* and *Udea rubigalis*) (Figs. 91, 93) . . . . . **Pyraustinae, Glaphyriinae, Evergestinae** 32

Note: Unless otherwise stated, the taxa following couplet 31 are **Pyraustinae**



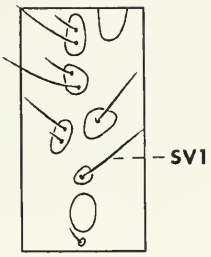
62

63

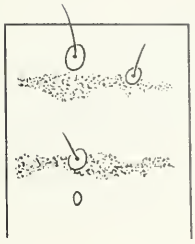
30. One subventral seta on meso- and metathorax (Fig. 64); body with 2 pink longitudinal stripes on each side (Fig. 65); pink-pigmented area around lateral setae on proleg-bearing segments . . . . . ***Eoreuma loftini*** (Dyar)

Distribution: Mexico and United States
Hosts: 1998: *Cymbopogon citratus, Saccharum officinarum*
pre-1998: corn, millet, rice, sorghum
Note: one SV seta also occurs in *Crambus*; see Rodriguez-del-Bosque et al. 1990

– Two subventral setae on meso- and metathorax (Fig. 66); body with or without pigmented stripes; no pigmented area around lateral setae on proleg-bearing segments 31



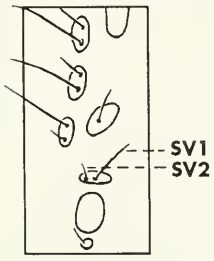
64



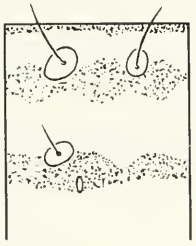
65

31. Body with pinkish middorsal stripe and two lateral stripes on each side (Fig. 67); setal pinacula concolorous with body . . . . . ***Chilo suppressalis*** (Walker)

Distribution: Europe, Middle East, Southeast Asia to India, Oceania; adventive in Hawaii
Hosts: 1998: *Cymbopogon citratus*
pre-1998: cabbage, corn, eggplant, millet, rice straw, sugarcane, sorghum, tomatoes, and wheat, many others
Note: see Bleszynski 1970, Meijermann and Ulenberg 1996, Whittle and Ferguson 1988



66

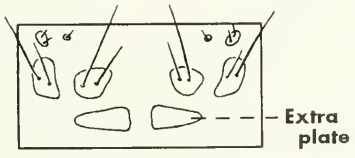


67

– Body with or without lateral stripes, but without pinkish middorsal stripe; setal pinacula concolorous with body (winter form) or darkly pigmented (summer form) . . . . . ***Diatraea*** spp.

Distribution: tropical Western Hemisphere including southern U.S.
Hosts: 1998: *Musa* sp., *Saccharum officinarum, Zea mays*
pre-1998: rice, sorghum
Note: Some species of *Chilo* will key to *Diatraea* based on color pattern (Passoa, pers. comm.), but *Diatraea* does not occur in the Old World; see Box 1931, Dyar and Heinrich 1927

32. Meso- and metathorax without nonsetal bearing plates posterior to dorsal pinacula 33
– Meso- and metathorax with a pair of nonsetal bearing plates posterior to dorsal pinacula (Fig. 68) . . . 34



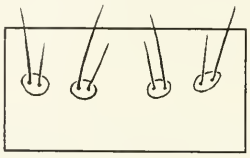
68

33. Small pinacula anterior to dorsal and subdorsal pinacula bearing microscopic setae (also occurring in *L. orbonalis*, see couplet 50) (Fig. 68) . . . . . **Pyrausta** sp.

Distribution: cosmopolitan

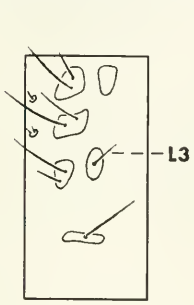
Hosts: 1998: *Allium cepa, Citrullus lanatus, Mentha* sp., *Momordica charantia, Ocimum* sp., *Ocimum basilicum, Origanum* sp., *Thymus* sp., *Thymus vulgaris*
pre-1998: *Amaranthus* sp.
Note: According to Allyson (1981b) last instar larvae are characterized by 2 or 3 SV setae on A1, prothoracic shield lightly pigmented, pinacula below spiracles with paler pigmentation than those above spiracles, body at most 20 mm long; although the genus is cosmopolitan, most of the interceptions on the host plants are from the tropical Western Hemisphere

– No small pinacula anterior to dorsal and subdorsal pinacula (Fig. 69) 36

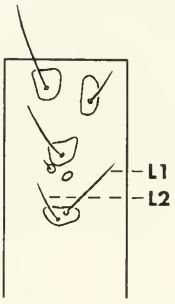


69

34. No extra nonsetal bearing plate below seta L3 on meso- and metathorax (Fig. 70) and behind L1 and L2 on abdominal segments 1 to 7 (Fig. 71) 35



70



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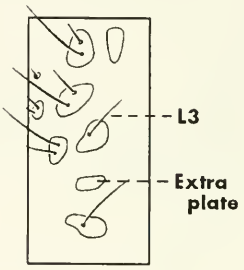

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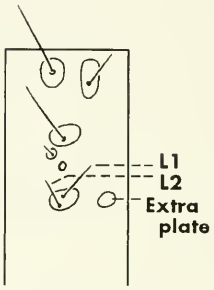
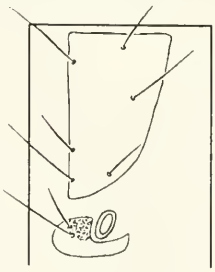


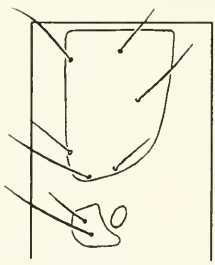
73

– An extra nonsetal bearing plate below seta L3 on meso- and metathorax (Fig. 72) and behind L1 and L2 on A1 to A7 (Fig. 73) . . . . . ***Conogethes*** spp.

Distribution: southeast Asia, including India and Pakistan, Australia; does not occur in Hawaii
Hosts: *Castanea* sp., *Dimocarpus longan, Gardenia* sp., *Nephelium lappaceum, Psidium guajava, Pyrus communis, Syzgium malacense*
pre-1998: *Catalpa*, peach, pine
Note: prespiracular shield of prothorax extending below and beyond spiracle (Fig. 74); this species was known as *Dichocrocis punctiferalis* (Guenée); *C. punctiferalis* is a complex of species (unpublished).



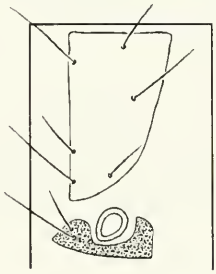
74



75

35. Prespiracular shield of prothorax crescent shaped extending below spiracle (Fig. 75) . . . . . *Maruca vitrata* (Fabricius)

Distribution: Africa, Asia, Australia, Mexico to South America, adventive in Hawaii
Hosts: 1998: *Phaseolus lunatus, Phaseolus vulgaris, Vigna* sp.
pre-1998: beans, legumes, peas, pigeon peas
Note: this species was known as *Maruca testulalis* (Geyer); there are a few records of adults captured in the southern U.S; synonymized by Munroe et al. 1995; see also Ferguson, not dated



76

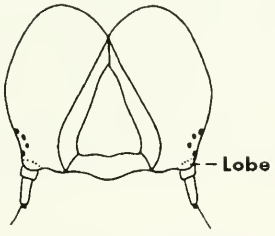
– Prespiracular shield of prothorax extending below and behind spiracle (Fig. 76) . . . . . ***Megastes*** sp.

Distribution: West Indies
Host: sweet potato

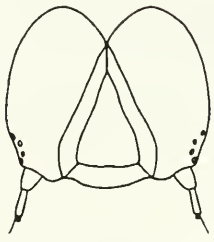
36. Head capsule with a lobelike extension over base of antenna (Fig. 77) . . . . . ***Ostrinia nubilalis*** (Hübner)

Distribution: Europe and United States
Hosts: 1998: *Capsicum* sp., *Malus* sp., strawberries, *Zea mays*
pre-1998: beans, beets, celery, clover, cucumbers, eggplant, lettuce, peas, potatoes, rhubarb, string beans, tomatoes, wheat
Note: see Heinrich 1919, Allyson 1981b

– Head capsule without a lobelike extension over base of antenna (Fig. 78) 37



77



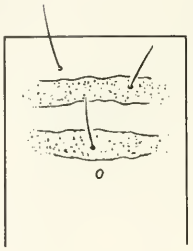
78

37. Dorsal and subdorsal setae of the abdominal segments on strongly conical black chalazae . . . . . **Evergestinae, *Evergestis rimosalis*** (Guenée)

Distribution: Western Hemisphere
Hosts: 1998: *Brassica* sp.
pre-1998: Brassicaceae, including cabbage, brussels sprouts, cauliflower, watercress
Note: it should be reported as "probably *E. forficalis* (L.)" if the origin is Europe; see Munroe 1973

– Abdominal segments without conical black chalazae 38

38. Body with pinkish longitudinal stripes (Fig. 79) 39
– Body without pinkish longitudinal stripes 40



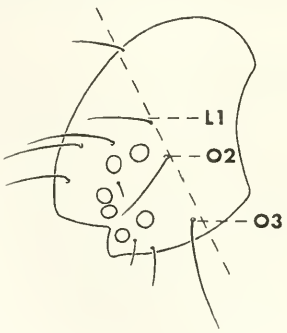
79

39. Head blackish or brownish with whitish areas along adfrontal sutures extending to vertex, seta O3 anterior to a line joining setae L1 and O2 (Fig. 80) . . . . . **Glaphyriinae**, ***Hellula rogatalis*** (Hulst)

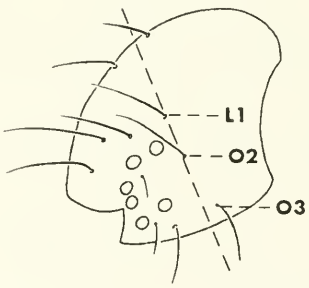
Distribution: Western Hemisphere; does not occur in Hawaii
Hosts: *Brassica oleracea, Brassica rapa*
pre-1998: mustard, radish, other Brassicaceae
Note: should be reported as "probably *H. undalis* (F.)" if the origin is the Old World; see Munroe 1972, Allyson 1981a

– Head pale, mottled, area along adfrontal sutures pale but not white, seta O3 posterior to a line joining setae L1 and O2 (Fig. 81) . . . . . **Glaphyriinae, *Hellula phidilealis*** (Walker)

Distribution: Western Hemisphere; adventive in Hawaii
Hosts: *Brassica* sp., *Brassica oleracea, Brassica pekinensis, Brassica rapa, Raphanus sativus, Spinacia oleracea*
pre-1998: white chard, and other Brassicaceae
Note: see Munroe 1972



80

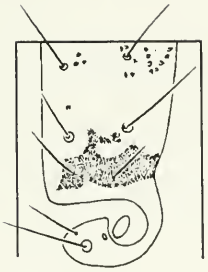


81

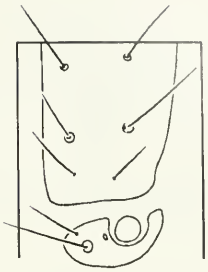
40. Prespiracular shield of prothorax extending below and behind spiracle (Figs. 82, 83) 41
– Prespiracular shield of prothorax not extending below and behind spiracle, but may completely enclose the spiracle (Figs. 85, 87) 42

41. Prothorax with sclerotization extending from posterolateral margin of prothoracic shield behind and below spiracle to prespiracular shield (Fig. 82) . . . . . ***Achyra rantalis*** (Guenée)

Distribution: Mexico, West Indies, and United States
Hosts: *Medicago sativa, Rosa* sp., *Sesuvium* sp.
pre-1998: beets, cotton, soybeans, and many others
Note: see Allyson 1976, 1981b



82

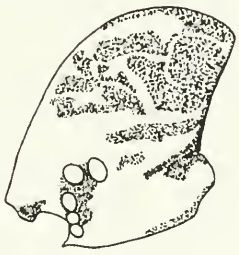


83

– Prespiracular shield of prothorax extending below and behind spiracle, not fused with posterolateral margin of prothoracic shield (Fig. 83) . . . . . ***Loxomorpha flavidissimalis*** Grote

Distribution: Mexico
Hosts: cactus

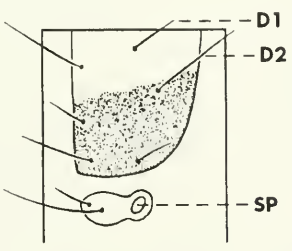
42. Head yellow with dark pattern (Fig. 84); prothoracic shield broadly shaded laterally (Figs. 85, 87) . . . 43
– Head not patterned; prothoracic shield without dark shading laterally 44



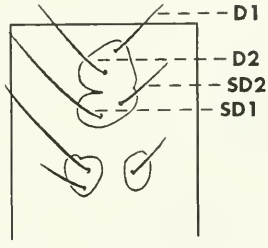
84

43. Prespiracular shield enclosing the spiracle (Fig. 85); A1 with SV trisetose; prothoracic shield with dark lateral shading extending to seta D2 (Fig. 85); dorsal and subdorsal pinacula of mesothorax fused (sometimes not fused in early instars) (Fig. 86) . . . . . ***Herpetogramma bipunctalis*** (Fabricius)

Distribution: Western Hemisphere
Hosts: 1998: *Amaranthus* sp., *Amaranthus caudatus, Corchorus olitorius, Gomphrena* sp., *Jatropha* sp., *Spinacia* sp., *Strobilanthes* sp., *Xanthosoma brasiliense*
pre-1998: alfalfa, beets, cotton, soybeans
Note: see Allyson 1984



85

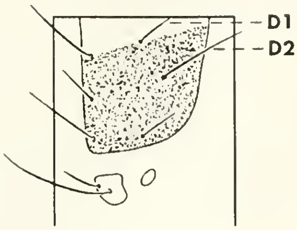


86

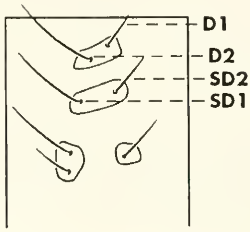
– Prespiracular shield not enclosing the spiracle (Fig. 87); A1 with SV setae bisetose; dorsal and subdorsal pinacula of mesothorax usually not fused (Fig. 88) . . . . . ***Rhectocraspeda periusalis*** (Walker)

Distribution: West Indies and United States
Hosts: 1998: *Amaranthus* sp., *Momordica charantia, Strobilanthes* sp.
pre-1998: Solanaceae, including eggplant, potatoes, and tomatoes
Note: *Pilemia* Möschler is a junior synonym of *Rhectocraspeda* Warren, new combination in Munroe et al. 1995

44. Prothoracic shield with at least one dark reniform spot posterior to seta XD2 (Figs. 90, 92) 45
– Prothoracic shield without dark reniform spot posterior to seta XD2 47



87

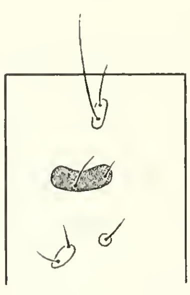


88

45. D1 and D2 on mesothorax on the same sclerotized pinaculum (Fig. 89) . . ***Spoladea recurvalis*** Fabricius

Distribution: cosmopolitan, adventive in Hawaii
Hosts: 1998: *Amaranthus* sp., *Amarantus recurvalis, Celosia* sp., *Chrysanthemum* sp., *Colocasia* sp., *Eryngium foetidum, Eupatorium* sp., *Impatiens* sp., *Jatropha curcas, Mentha* sp., *Phytolacca americana, Polygonum perfoliatum, Spinacia* sp., *Spinacia oleracea, Xanthosoma* sp., *Zea mays*
pre-1998: Amaranthaceae, Areca palm, Asteraceae, beets, Chenopodiaceae, soybeans, swiss chard
Note: see Allyson 1984

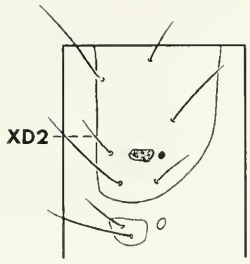
– D1 and D2 on mesothorax on separate, unsclerotized pinacula 46



89

46. Prespiracular shield ovate (Fig. 90); crochets triordinal on mesal aspect (Fig. 91) .... ***Udea rubigalis*** (Guenée)

Distribution: Canada south to Costa Rica
Hosts: *Amaranthus* sp., *Ipomoea* sp., *Mentha* sp., *Ocimum* sp., *Ocimum basilicum, Pimenta dioica, Raphanus sativus, Spinacea oleracea*
pre-1998: alfalfa, cabbage, celery, *Chrysanthemum*, clover, cucumbers, lettuce, peas, roses, sugar beets, sweet potato
Note: should be reported as "probably *Udea ferrugalis* (Hübner)" if the origin is Europe; see Allyson 1984

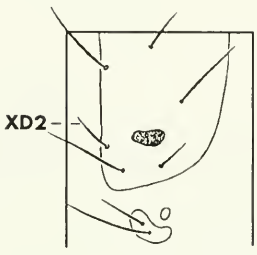


90

91

– Prespiracular shield crescent shaped extending below spiracle (Fig. 92); crochets biordinal on mesal aspect (Fig. 93) . . . . . ***Lineodes integra*** (Zeller)

Distribution: United States, Mexico, West Indies
Hosts: 1998: *Capsicum* sp., *Lycopersicon lycopersicon, Physalis ixocarpa, Physalis peruviana, Solanum torvum*
pre-1998: Solanaceae, including eggplant

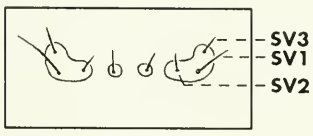


92

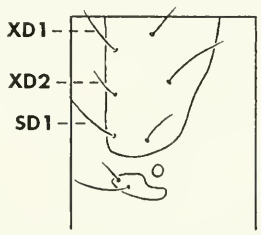
93

47. A1 with three subventral setae (Fig. 94); prothorax with seta XD2 equidistant from setae SD1 and XD1 (Fig. 95); crochets biordinal (Fig. 96) . . . . . ***Hendecasis duplifascialis*** Hampson

Distribution: southeastern Asia, does not occur in Hawaii
Hosts: 1998: *Dianthus* sp., *Gardenia* sp., *Jasminium sambac*, Orchidaceae, *Plumeria rubra, Polianthes tuberosa*
pre-1998: jasmine



94



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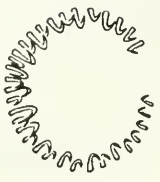
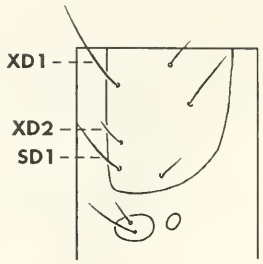


96

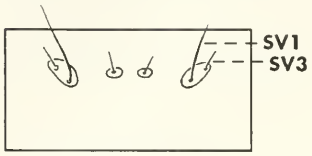
– A1 with less than three subventral setae (Figs. 99, 101); prothorax with seta XD2 closer to seta SD1 than to seta XD1 (Fig. 97); crochets triordinal (Fig. 98) 48



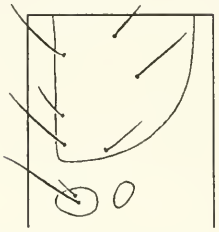
97

98

48. A1 with two subventral setae (Fig. 99); prespiracular shield oblong (Fig. 100) 49

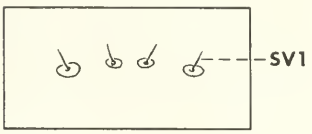


99



100

— A1 with one subventral seta (Fig. 101); prespiracular shield crescent shaped, may extend under spiracle (Fig. 102); pinaculum of seta D1 on A2 to A8 with dark spot on anterior margin (Fig. 103) 50



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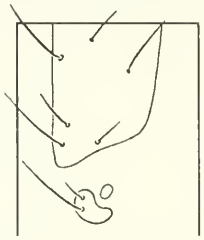
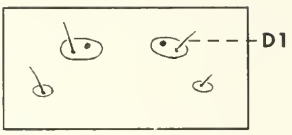


102



103

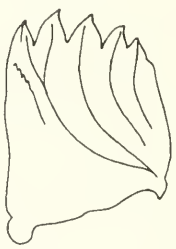
49. Head with a pigmented spot at genal angle (Fig. 104); mandible without a projection on lateral margin (Fig. 105); pinacula dark on early instars, pale in later instars . . . . . ***Diaphania nitidalis*** (Stoll)

Distribution: Western Hemisphere

Hosts: 1998: *Cucumis* sp., *Cucumis melon, Cucumis sativus, Cucurbita* sp., *Cucurbita pepo, Sechium edule*

pre-1998: Cucurbitaceae, including gourds, melons, *Momordica* sp., squash

104



105

– Head without pigmented spot at genal angle; mandible with a projection on lateral margin (Fig. 106); pinacula concolorous with body in all instars . . . . . *Diaphania indica* Saunders complex

Distribution: Western Hemisphere
Hosts: 1998: *Cucurbita* sp., *Fernaldia* sp., *Momordica charantia, Momordica balsamina, Murraya* sp., *Ocimum basilicum, Sechium edule, Thymus vulgaris*
pre-1998: Cucurbitaceae, including cucumbers, cantaloupe, gourds, melons, pumpkins, squash
Note: to separate pupae of *D. hyalinata* (L.) from *D. indica* (Saunders): proboscis extends to A7 in *indica* and to A8 or A9 in *hyalinata*; *hyalinata* occurs from Canada south to Argentina, *indica* is cosmopolitan, in the Western Hemisphere occurring from Florida to South America; see Whittle and Ferguson 1987a, Clavijo 1990

106

50. Head, prothoracic shield, and body pinacula brownish yellow, not concolorous . . . . . ***Leucinodes orbonalis*** (Guenée)

Distribution: Africa and Southeast Asia, does not occur in Hawaii
Hosts: 1998: *Capsicum* sp., *Punica granatum, Solanum* sp., *Solanum melongena*
pre-1998: chayote, potatoes, Solanaceae, tomatoes
Note: The character that separates *L. orbonalis* from *N. elegantalis*, the presence of a dark spot on the anterior margin of the pinaculum of seta D1 of A2 to A8, was found to occur in both species; no adults of this species have been observed from the Western Hemisphere; see Whittle and Ferguson 1987b

– Head and prothoracic shield pale yellow, pinacula concolorous with body . . . . . ***Neoleucinodes elegantalis*** (Guenée)

Distribution: Mexico to South America, and West Indies
Hosts: 1998: *Capsicum* sp., *Capsicum annuum, Lycopersicon* sp., *Lycopersicon esculentum, Sechium edule, Solanum* sp., *Solanum melongena, Solanum quitoense, Solanum torvum*
pre-1998: Solanaceae

Table 2. Hosts and pyraloid larvae.

Hosts	Pyraloid Species
Abelmoschus esculentus (see okra)	
Acacia	*Corcyra cephalonica*
Acanthocereus	*Ephestia elutella*
Alfalfa [*Medicago sativa*]	*Achyra rantalis*
	Elasmopalpus lignosellus
	Ephestia elutella
	Herpetogramma bipunctalis
	Udea rubigalis
Allium	*Ephestia elutella*
	Pyralis farinalis
Allium cepa (onion)	

Table 2. Continued.

Hosts	Pyraloid Species
Allium sativum (see garlic)	
allspice	*Udea rubigalis*
Amaranthaceae (see *Amaranthus, Celosia*)	
Amaranthus	*Cryptoblabes*
	Herpetogramma bipunctalis
	Pyrausta
	Rhectocraspeda periusalis
	Spoladea recurvalis
	Udea rubigalis
Amaranthus caudatus (see lnea wheat)	
Anacardium	*Cadra cautella*
Ananas comosus (see pineapple)	
Annona	*Amyelois transtilla*
	Ectomyelois ceratoniae
	Ephestia kuehniella
Apium graveolens (see celery)	
apple [*Malus*]	*Amyelois transtilla*
	Ostrinia nubilalis
Arabian jasmine [*Jasminium sambac*]	*Hendecasis duplifascialis*
Arachis	*Corcyra cephalonica*
Arachis hypogaea (see peanuts)	
Areca catechu (see areca nut, betel nut)	
areca nut, betel nut [*Areca catechu*]	*Paralipsa gularis*
Areca palm [*Chrysalidocarpus*]	*Cadra cautella*
	Spoladea recurvalis
Armoracia rusticana (see horseradish)	
ash gourd [*Benincasa hispida*]	*Phidotricha erigens*
Asparagus officinalis (see asparagus)	
asparagus [*Asparagus officinalis*]	*Elasmopalpus lignosellus*
Asteraceae	*Homoeosoma electellum*
	Spoladea recurvalis
avocado [*Persea americana*]	*Aglossa caprealis*
Bambusa	*Cadra cautella*
	Paralipsa gularis
bastard cedar [*Guazuma ulmifolia*]	*Corcyra cephalonica*
	Paralipsa gularis
basil [*Ocimum basilicum*]	*Diaphania indica* complex
	Pyrausta
	Udea rubigalis
beans (many genera & species)	*Elasmopalpus lignosellus*
	Fundella pellucens
	Maruca vitrata
	Ostrinia nunbilalis
	Udea rubigalis
beans, dried	*Cadra figulilella*
beets [*Beta vulgaris*]	*Achyra rantalis*
	Herpetogramma bipunctalis
	Ostrinia nubilalis
	Spoladea recurvalis
	Udea rubigalis
bell pepper [*Capsicum annuum*]	*Etiella zinckenella*
	Neoleucinodes elegantalis
	Paralipsa gularis
	Plodia interpunctella

Table 2. Continued.

Hosts	Pyraloid Species
Benincasa hispida (see ash gourd)	
Berberis	*Cadra cautella*
	Plodia interpunctella
Beta vulgaris (see beets, white chard)	
Bidens	*Homoeosoma electellum*
black walnut [*Juglans nigra*]	*Ectomyelois ceratoniae*
	Ephestia elutella
Brassica (see mustard)	
Brassica napus, B. rapa (see turnip)	
Brassica oleracea (see brussels sprouts, cabbage, cauliflower)	
Brassica pekinensis (see Chinese cabbage)	
Brassicaceae (see cabbage, turnips, brussels sprouts, cauliflower, mustard)	
broad bean [*Vicia faba*]	*Plodia interpunctella*
brussels sprouts [*Brassica oleracea*]	*Evergestis rimosalis*
	Hellula phidilealis
	Hellula rogatalis
butter beans [*Phaseolus lunatus*]	*Etiella zinckenella*
	Maruca vitrata
	Mussidia nigrivenella
cabbage [*Brassica oleracea*]	*Chilo suppressalis*
	Evergestis rimosalis
	Hellula phidilealis
	Hellula rogatalis
	Udea rubigalis
Cabomba (see fanwort)	
cacao [*Theobroma cacao*]	*Cadra cautella*
	Mussidia nigrivenella
cactus [*Opuntia*]	*Etiella zinckenella*
	Loxomorpha flavidissimalis
Caesalpinia pulcherrima (see dwarf poinciana)	
Cajanus cajan (see pigeon peas)	
calabar beans [*Physostigma venenosum*]	*Mussidia nigrivenella*
Calophyllum brasiliense (see Santa Maria, galba)	
Camellia sinensis (see tea)	
cantaloupe [*Cucumis melo*]	*Diaphania indica* complex
	Diaphania nitidalis
Capsicum	*Cadra cautella*
	Cadra figulilella
	Ectomyelois ceratoniae
	Ephestia elutella
	Leucinodes orbonalis
	Lineodes integra
	Neoleucinodes elegantalis
	Ostrinia nubilalis
	Plodia interpunctella
Capsicum annuum (see bell pepper)	
Carapa guianensis (see crabwood)	
Carica papaya (see papaya)	
carob [*Ceratonia siliqua*]	*Cadra calidella*
	Ectomyelois ceratoniae
	Mussidia nigrivenella
	Paralipsa gularis

Table 2. Continued.

Hosts	Pyraloid Species
Cassia (see cassia)	
Cassia fistula (see golden shower tree)	
Cassia grandis	*Trachylepidia fructicassiella*
cassia [*Cassia*]	*Corcyra cephalonica*
	Paralipsa gularis
	Trachylepidia fructicassiella
Castanea (see chestnut)	
Castanea sativa (see European chestnut)	
Catalpa	*Conogethes*
cat-claw mimosa [*Mimosa pigra*]	*Elasmopalpus lignosellus*
	Phidotricha erigens
cat-tail [*Typha latifolia*]	Schoenobiinae
cauliflower [*Brassica oleracea*]	*Evergestis rimosalis*
	Hellula phidilealis
	Hellula rogatalis
Cedrela (see Spanish cedar)	
celery [*Apium graveolens*]	*Ostrinia nubilalis*
	Udea rubigalis
	Spoladea recurvalis
Celosia	
Ceratonia siliqua (see carob)	
cereal products	*Ephestia elutella*
Cereus	*Ectomyelois ceratoniae*
	Diaphania nitidalis
	Leucinodes orbonalis
	Neoleucinodes elegantalis
Chaenomeles japonica	*Cryptoblabes*
chayote [*Sechium edule*]	*Diaphania indica* complex
Chenopodiaceae (see spinach, beets, swiss chard)	
cherry tomato [*Physalis peruviana*]	*Lineodes integra*
chestnut [*Castanea*]	*Cadra calidella*
	Conogethes
	Ephestia elutella
	Paralipsa gularis
chickpeas [*Cicer arietinum*]	*Ancylostomia stercorea*
	Etiella zinckenella
	Plodia interpunctella
Chimonanthus	*Ectomyelois ceratoniae*
Chinese cabbage [*Brassica pekinensis*]	*Hellula phidilealis*
Chinese pear [*Pyrus pyrifiora*]	*Ectomyelois ceratoniae*
Chrysalidocarpus (see areca palm)	
Chrysanthemum	*Spoladea recurvalis*
	Udea rubigalis
Chrysophyllum	*Ephestia kuehniella*
Cicer arietinum (see chickpeas)	
Citrullus lanatus (see watermelon)	
Citrus	*Cadra cautella*
Citrus sinensis (see oranges)	
Cleome (see spider-plant)	
clover [*Trifolium*]	*Ostrinia nubilalis*
	Udea rubigalis
cocoa beans [*Theobroma cacao*]	*Corcyra cephalonica*
Coffea arabica (see coffee)	
coffee [*Coffea arabica*]	*Cadra cautella*
	Corcyra cephalonica
	Elasmopalpus lignosellus

Table 2. Continued.

Hosts	Pyraloid Species
Cola	*Corcyra cephalonica*
Coleus (see *Plectranthus*)	
Colocasia	*Spoladea recurvalis*
Compositae (see Asteraceae)	
Corchorus olitorius (see tossa jute)	
corn [*Zea mays*]	*Amyelois transtilla*
	Cadra cautella
	Chilo suppressalis
	Diatraea
	Ectomyelois ceratoniae
	Elasmopalpus lignosellus
	Etiella zinckenella
	Eoreuma loftini
	Hypsipyla
	Moodna bisinuella
	Ostrinia nubilalis
	Paralipsa gularis
	Phidotricha erigens
	Spoladea recurvalis
Corylus avellana (see European filbert, Europen hazelnut)	
cotton [*Gossypium*]	*Achrya rantalis*
	Herpetogramma bipunctalis
	Homoeosoma electellum
	Phidotricha erigens
cow peas [*Vigna unguiculata*]	*Ancylostomia stercorea*
	Elasmopalpus lignosellus
	Fundella pellucens
	Maruca vitrata
	Trachylepidia fructicassiella
crabapple [*Malus sylvestris*]	*Amyelois transtilla*
	Ectomyelois ceratoniae
crabwood [*Carapa guianensis*]	*Hypsipyla*
Cruciferae (see Brassicaceae)	
cucumbers [*Cucumis sativa*]	*Diaphania indica* complex
	Diaphania nitidalis
	Ostrinia nubilalis
	Udea rubigalis
Cucumis	*Diaphania nitidalis*
Cucumis melo (see cantaloupe)	
Cucumis sativus (see cucumber)	
Cucurbita (see gourds, squash)	*Cadra cautella*
	Diaphania indica complex
	Diaphania nitidalis
	Ectomyelois ceratoniae
	Etiella zinckenella
	Paralipsa gularis
Cucurbita pepo (see pumpkin)	
Cucurbitaceae (see squash, cantaloupes, cucumbers, gourds, pumpkins)	
cumin [*Cuminum*]	*Corcyra cephalonica*
Cuminum (see cumin)	
Cydonia oblonga (see quince)	
Cymbopogon citratus (see lemon grass)	
Cyperus papyrus (see papyrus)	

Table 2. Continued.

Hosts	Pyraloid Species
dates [*Phoenix*]	*Cadra calidella*
	Cryptoblabes
	Ectomyelois ceratoniae
date palm [*Phoenix dactylifera*]	*Cadra cautella*
	Cadra figulilella
	Ectomyelois ceratoniae
	Paralipsa gularis
Dennetia	*Ephestia kuehniella*
Dianthus (see pink)	
Dimocarpus longan (see longan)	
dried foodstuffs	*Cadra calidella*
dried fruits	*Cadra calidella*
	Cadra figulilella
dried seeds	*Cadra figulilella*
dried vegetable products	*Cadra cautella*
	Ephestia elutella
	Ephestia kuehniella
	Pyralis farinalis
	Trachylepidia fructicassiella
dunnage	*Paralipsa gularis*
dwarf poinciana [*Caesalpinia pulcherrima*]	*Amyelois transtilla*
eggplant [*Solanum melongena*]	*Chilo suppressalis*
	Leucinodes orbonalis
	Lineodes integra
	Neoleucinodes elegantalis
	Ostrinia nubilalis
	Rhectocraspeda periusalis
Elasis	*Paralipsa gularis*
Eriobotrya japonica (see loquat)	
Eryngium foetidum	*Spoladea recurvalis*
Eupatorium	*Spoladea recurvalis*
European chestnut [*Castanea sativa*]	*Cadra figulilella*
	Ectomyelois ceratoniae
	Etiella zinckenella
	Plodia interpunctella
European filbert, European hazelnut [*Corylus avellana*]	*Elasmopalpus lignosellus*
Fabaceae (see legumes)	
Fanwort (*Cabomba*)	*Parapoynx*
Fernaldia	*Diaphania indica* complex
Ficus	*Cadra calidella*
	Cadra figulilella
Ficus carica (see fig)	
Fig [*Ficus carica*]	*Cadra calidella*
	Cadra figulilella
	Ectomyelois ceratoniae
	Plodia interpunctella
foodstuffs	*Pyralis farinalis*
Fragaria (see strawberries)	
Gardenia	*Conogethes*
	Hendecasis duplifascialis
garlic [*Allium sativum*]	*Aglossa caprealis*
	Cadra cautella
	Cadra figulilella

Table 2. Continued.

Hosts	Pyraloid Species
Gleditsia	*Plodia interpunctella*
Glycine max (see soybeans)	
golden shower tree [*Cassia fistula*]	*Trachylepidia fructicassiella*
Gomphrena	*Herpetogramma bipunctalis*
Gossypium (see cotton)	
Gossypium hirsutum (see upland cotton)	
gourds [*Cucurbita*]	*Diaphania indica* complex
	Diaphania nitidalis
grain (damp)/fungus	*Aglossa caprealis*
grapes [*Vitis*]	*Cryptoblabes*
	Ephestia elutella
	Plodia interpunctella
guajava or guava [*Psidium guajava*]	*Cadra cautella*
	Cadra figulilella
	Conogethes
	Cryptoblabes
	Ectomyelois ceratoniae
Guazuma ulmifolia (see bastard cedar)	
guizotia [*Guizotia abyssinical*]	*Cadra cautella*
Guizotia abyssinica (see guizotia)	
Helianthus annuus (see sunflower)	
Hibiscus (see mallow)	
horseradish [*Armoracia rusticana*]	*Trachylepidia fructicassiella*
horse-radish tree [*Moringa oleifera*]	*Ephestia kuehniella*
Hydrilla	*Parapoynx*
Hygrophila	*Parapoynx*
Impatiens	*Spoladea recurvalis*
Inca wheat [*Amaranthus caudatus*]	*Herpetogramma bipunctalis*
Inga	*Corcyra cephalonica*
	Trachylepidia fructicassiella
Ipomoea	*Udea rubigalis*
Ipomoea batatas (see sweet potato)	
jasmine [*Jasminium*]	*Hendecasis duplifascialis*
Jasminium (see jasmine)	
Jasminium sambac (see Arabian jasmine)	
Jatropha	*Herpetogramma bipunctalis*
Jatropha curcas (see physic nut)	
Johnson grass [*Sorghum halapense*]	*Elasmopalpus lignosellus*
Juglans (see walnuts)	
Juglans nigra (see black walnut)	
jujube [*Ziziphus jujuba*]	*Plodia interpunctella*
lablab bean [*Lablab pupureus*]	*Etiella zinckenella*
Lablab pupureus (see lablab bean)	
Lactuca (see lettuce)	
langsat [*Lansium domesticum*]	*Ectomyelois ceratoniae*
	Paralipsa gularis
Lansium domesticum (see langsat)	
legumes	*Ectomyelois ceratoniae*
	Etiella zinckenella
	Maruca vitrata
Leguminosae (see Fabaceae)	
Lemon grass [*Cymbopogon citratus*]	*Chilo suppressalis*
	Eoreuma loftini
Lens	*Corcyra cephalonica*

Table 2. Continued.

Hosts	Pyraloid Species
lettuce [*Lactuca*]	*Ostrinia nubilalis*
	Udea rubigalis
lima beans [*Phaseolus lunatus*]	*Etiella zinckenella*
	Fundella pellucens
	Maruca vitrata
	Phidotricha erigens
Limnophila	*Parapoynx*
locust bean (see carob)	
longan [*Dimocarpus longan*]	*Conogethes*
	Cryptoblabes
loosestrife [*Lythrum*]	*Cryptoblabes*
	Conogethes
loquat [*Eriobotrya japonica*]	*Phidotricha erigens*
Lycopersicon	*Neoleucinodes elegantalis*
Lycopersicon esculentum (= *L. lycopersicon*) (see tomatoes)	
Lythrum (see loosestrife)	
mahogany [*Swietenia*]	*Hypsipyla*
mallow [*Hibiscus*]	*Conogethes*
Malus (see apple)	
Malus sylvestris (see crabapple)	
Mammea	*Phidotricha erigens*
Mangifera indica (see mango)	
mango [*Mangifera indica*]	*Amyelois transtilla*
	Ectomyelois ceratoniae
	Phidotricha erigens
Manihot esculenta (see manioc)	
Manila tamarind [*Pithecellobium dulce*]	*Cadra cautella*
	Ectomyelois ceratoniae
manioc [*Manihot esculenta*]	*Cadra figulilella*
Maranta	*Elasmopalpus lignosellus*
Medicago arabica (see clover)	
Medicago sativa (see alfalfa)	
melons [*Cucumis melo*]	*Diaphania indica* complex
	Diaphania nitidalis
Mentha	*Elasmopalpus lignosellus*
	Pyrausta
	Spoladea recurvalis
	Udea rubigalis
millet [*Panicum miliaceum*]	*Chilo suppressalis*
	Eoreuma loftini
Mimosa pigra (see cat-claw mimosa)	
Momordica	*Diaphania nitidalis*
Momordica balsamina	*Diaphania indica* complex
Momordica charantia	*Diaphania indica* complex
	Diaphania nitidalis
	Pyrausta
	Rhectocraspeda periusalis
Moinga oleifera (see horse-radish tree)	
Morus	*Cadra calidella*
	Cadra cautella
	Cadra figulilella
	Plodia interpunctella
Murraya	*Diaphania indica* complex
Musa	*Cryptoblabes*
	Diatraea

Table 2. Continued.

Hosts	Pyraloid Species
mustard [*Brassica*]	*Corcyra cephalonica*
	Ephestia elutella
	Evergestis rimosalis
	Hellula phidilealis
	Hellula rogatalis
	Paralipsa gularis
Myriophyllum	*Parapoynx*
naranjilla [*Solanum quitoense*]	*Neoleucinodes elegantalis*
Narcissus tazetta (see polyanthus narcissus)	
Nephelium lappaceum (see rambutan)	
nosegay [*Plumeria rubra*]	*Hendecasis duplifascialis*
nuts (stored)	*Cadra calidella*
	Cadra figulilella
	Ectomyelois ceratoniae
Ocimum	*Udea rubigalis*
	Pyrausta
Ocimum basilicum (see basil)	
okra [*Abelmoschus esculentus*]	*Corcyra cephalonica*
Oncidium	*Paralipsa gularis*
onion [*Allium cepa*]	*Pyrausta*
Opuntia (see cactus)	
oranges [*Citrus sinensis*]	*Amyelois transtilla*
	Cryptoblabes
	Homoeosoma electellum
Orchidaceae	*Hendecasis duplifascialis*
Origanum	*Pyrausta*
Oryza	*Corcyra cepalonica*
	Plodia interpunctella
Oryza sativa (see rice)	
packing	*Aglossa caprealis*
	Pyralis farinalis
Paeonia (see peony)	
Panicum miliaceum (see millet)	
papaya [*Carica papaya*]	*Cadra cautella*
papyrus [*Cyperus papyrus*]	*Paralipsa gularis*
Parkia	*Etiella zinckenella*
peach [*Prunus persica*]	*Amyelois transtilla*
	Conogethes
	Plodia interpunctella
peanuts [*Arachis hypogaea*]	*Cadra cautella*
pear [*Pyrus communis*]	*Amyelois transtilla*
	Cadra cautella
	Conogethes
	Ectomyelois ceratoniae
peas [*Pisum sativum*]	*Ancylostomia stercorea*
	Cadra cautella
	Elasmopalpus lignosellus
	Etiella zinckenella
	Fundella pellucens
	Maruca vitrata
	Ostrinia nubilalis
	Udea rubigalis

Table 2. Continued.

Hosts	Pyraloid Species
peony [*Paeonia*]	*Amyelois transtilla*
Persea americana (see avocado)	
Petiveria alliacea	*Phidotricha erigens*
Phaseolus	*Cadra cautella*
	Ectomyelois ceratoniae
	Plodia interpunctella
Phaseolus lunatus (see butter beans, lima beans)	
Phaseolus vulgaris (see string beans)	
Phoenix (see dates)	
Phoenix dactylifera (see date palm)	
Physalis ixocarpa (see tomatillo)	
Physalis peruviana (see cherry tomato)	
physic nut [*Jatropha curcas*]	*Spoladea recurvalis*
Physostigma venenosum (see calabar beans)	
Phytolacca americana (see pokeweed)	
pigeon peas [*Cajanus cajan*]	*Ancylostomia stercorea*
	Amyelois transtilla
	Etiella zinckenella
	Fundella pellucens
	Maruca vitrata
Pimenta dioica (see allspice, pimento)	
pimento	*Udea rubigalis*
pine [*Pinus*]	*Conogethes*
pineapple [*Ananas comosus*]	*Alpheias conspirata*
	Cadra cautella
	Cryptoblabes
	Elasmopalpus lignosellus
	Genopaschia protomis
	Paralipsa gularis
pink [*Dianthus*]	*Hendecasis duplifascialis*
Pinus (see pine)	
Pista stratiotes (see water-lettuce)	
Pistacia	*Plodia interpunctella*
Pisum sativum (see peas)	
Pithecellobium dulce (see manila tamarind)	
Plectranthus	*Cadra calidella*
Plumeria rubra (see nosegay)	
Poaceae	*Plodia interpunctella*
pokeweed [*Phytolacca americana*]	*Spoladea recurvalis*
Polianthus tuberosa (see tuberose)	
polyanthus narcissus [*Narcissus tazetta*]	*Pyralis farinalis*
Polygonum perfoliatum	*Spoladea recurvalis*
pomegranate [*Punica granatum*]	*Amyelois transtilla*
	Cryptoblabes
	Ectomyelois ceratoniae
	Ephestia elutella
	Leucinodes orbonalis
	Paralipsa gularis
	Plodia interpunctella
potatoes [*Solanum tuberosum*]	*Ephestia elutella*
	Leucinodes orbonalis
	Ostrinia nubilalis
	Rhectocraspeda periusalis
Prosopis	*Plodia interpunctella*
Protea	*Ephestia elutella*

Table 2. Continued.

Hosts	Pyraloid Species
prune plum [*Prunus domestica*]	*Plodia interpunctella*
Prunus	*Cadra calidella*
	Cadra figulilella
	Ephestia elutella
Prunus avium (see sweet cherry)	
Prunus domestica (see prune plum)	
Prunus persica (see peach)	
Psidium guajava (see guajava or guava)	
pumpkin [*Cucurbita pepo*]	*Diaphania indica* complex
	Diaphania nitidalis
Punica granatum (see pomegranate)	
Pyrus communis (see pear)	
Pyrus pyriflora (see Chinese pear)	
quince [*Cydonia oblonga*]	*Amyelois transtilla*
	Ectomyelois ceratoniae
	Etiella zinckenella
radish [*Raphanus sativus*]	*Hellula phidilealis*
	Hellula rogatalis
	Udea rubigalis
raisins [*Vitis*]	*Cryptoblabes*
	Ephestia elutella
	Plodia interpunctella
rambutan [*Nephelium lappaceum*]	*Aglossa caprealis*
	Conogethes
	Paralipsa gularis
Randia	*Amyelois transtilla*
Raphanus sativus (see radish)	
Rheum rhubarbarum (see rhubarb)	
Rhododendron	*Paralipsa gularis*
rhubarb [*Rheum rhubarbarum*]	*Ostrinia nubilalis*
rice [*Oryza sativa*]	*Cadra cautella*
	Chilo suppressalis
	Corcyra cephalonica
	Diatraea
	Eoreuma loftini
	Ephestia elutella
	Paralipsa gularis
rice straw	see rice
Rorippa (see watercress)	
Rosa (see roses)	
rose, Malay apple [*Syzygium malaccense*]	*Conogethes*
roses [*Rosa*]	*Achyra rantalis*
	Cadra cautella
	Udea rubigalis
Rubus	*Cadra cautella*
Rumex	*Ancylostomia stercorea*
Saccharum officinarum (see sugarcane)	
Santa Maria, galba [*Calophyllum brasiliense*]	*Paralipsa gularis*
Sechium edule (see chayote)	
sesame [*Sesamum indicum*]	*Cadra cautella*
	Corcyra cephalonica
Sesamum indicum (see sesame)	
Sesbania	*Ectomyelois ceratoniae*
Sesuvium	*Achyra rantalis*
Sida	*Elasmopalpus lignosellus*
Solanaceae (see eggplant, potatoes, tomatoes)	

Table 2. Continued.

Hosts	Pyraloid Species
Solanum	*Leucinodes orbonalis*
	Neoleucinodes elegantalis
	Paralipsa gularis
Solanum melongena (see eggplant)	
Solanum quitoense (see naranjilla)	
Solanum torvum (see turkey berry)	
Solanum tuberosum (see potatoes)	
Sorghum (see sorghum)	
sorghum [*Sorghum*]	*Chilo suppressalis*
	Corcyra cephalonica
	Diatraea
	Elasmopalpus lignosellus
	Eoreuma loftini
	Phidotricha erigens
Sorghum bicolor (see sorghum)	
Sorghum halapense (see Johnson grass)	
soybeans [*Glycine max*]	*Achyra rantalis*
	Elasmopalpus lignosellus
	Herpetogramma bipunctalis
	Spoladea recurvalis
Spanish cedar [*Cedrela*]	*Hypsipyla*
spinach	*Hellula phidilealis*
	Spoladea recurvalis
	Udea rubigalis
Spinacia	*Herpetogramma bipunctalis*
	Spoladea recurvalis
Spinacia oleracea (see spinach)	
squash [*Cucurbita*]	*Diaphania indica* complex
	Diaphania nitidalis
Stirlingia	*Paralipsa gularis*
stored fruit products	*Plodia interpunctella*
stored grain (including cereals)	*Ephestia kuehniella*
	Mussidia nigrivenella
	Pyralis farinalis
	Plodia interpunctella
stored vegetable products (including seeds)	*Cadra cautella*
	Corcyra cephalonica
	Ephestia elutella
	Ephestia kuehniella
	Etiella zinckenella
	Mussidia nigrivenella
	Paralipsa gularis
	Plodia interpunctella
strawberries [*Fragaria*]	*Elasmopalpus lignosellus*
	Ostrinia nubilalis
string beans [*Phaseolus vulgaris*]	*Ancylostomia stercorea*
	Corcyra cephalonica
	Elasmopalpus lignosellus
	Etiella zinckenella
	Maruca vitrata
	Ostrinia nubilalis

Table 2. Continued.

Hosts	Pyraloid Species
Strobilanthes	*Herpetogramma bipunctalis*
	Rhectocraspeda periusalis
sugar beets (see beets)	
sugarcane [*Saccharum officinarum*]	*Cadra figulilella*
	Chilo suppressalis
	Diatraea
	Elasmopalpus lignosellus
	Eoreuma loftini
sunflower [*Helianthus annuus*]	*Homoeosoma electellum*
sweet cherry [*Prunus avium*]	*Cadra cautella*
	Cadra figulilella
	Ectomyelois ceratoniae
	Plodia interpunctella
sweet potato [*Ipomoea batatas*]	*Megastes*
	Udea rubigalis
Swietenia (see mahogany)	
swiss chard	*Spoladea recurvalis*
Syzygium malaccense (see rose or Malay apple)	
tamarind [*Tamarindus indica*]	*Amyelois transtilla*
	Cadra cautella
	Ectomyelois ceratoniae
	Phidotricha erigens
Tamarindus indica (see tamarind)	
tamarisk [*Tamarix*]	*Cryptoblabes*
Tamarix (see tamarisk)	
tea [*Camellia sinensis*]	*Plodia interpunctella*
Theobroma cacao (see cacao)	
thyme	*Diaphania indica* complex
	Pyrausta
Thymus	*Pyrausta*
Thymus vulgaris (see thyme)	
tomatillo [*Physalis ixocarpa*]	*Lineodes integra*
tomatoes [*Lycopersicon esculentum* (= *L. lycopersicon*)]	*Chilo suppressalis*
	Leucinodes orbonalis
	Lineodes integra
	Neoleucinodes elegantalis
	Ostrinia nubilalis
	Rhectocraspeda periusalis
tossa jute [*Corchorus olitorius*]	*Herpetogramma bipunctalis*
Trifolium (see clover)	
Triticum (see wheat)	
Tropaeolum majus (see nasturtium)	
tuberose [*Polyanthus tuberosa*]	*Hendecasis duplifascialis*
turkey berry [*Solanum torvum*]	*Lineodes integra*
	Neoleucinodes elegantalis
turnip [*Brassica napus, B. rapa*]	*Hellula phidilealis*
	Hellula rogatalis
Typha latifolia (see cat-tail)	
upland cotton [*Gossypium hirsutum*]	*Paralipsa gularis*
Vaccinium	*Cadra cautella*
Vallisneria	*Parapoynx*
vegetable (rotting)/fungus	*Aglossa caprealis*
Vicia faba (see broad bean)	
Vigna	*Maruca vitrata*
	Trachylepidia fructicassiella

Table 2. Continued.

Hosts	Pyraloid Species
Vigna unguiculata (see cow peas)	
Vitis (see grapes, raisins)	
Vitis vinifera (see wine grape)	
walnuts [*Juglans*]	*Amyelois transtilla*
watercress [*Rorippa*]	*Evergestis rimosalis*
water-lettuce [*Pista stratiotes*]	Schoenobiinae
watermelon [*Citrullus lanatus*]	*Pyrausta*
wheat [*Triticum*]	*Chilo suppressalis*
	Corcyra cephalonica
	Ostrinia nubilalis
white chard [*Beta vulgaris*]	*Hellula phidilealis*
wine grape [*Vitis vinifera*]	*Cadra calidella*
	Paralipsa gularis
Xanthosoma braziliense	*Herpetogramma bipunctalis*
	Spoladea recurvalis
Zea mays (see corn)	
Zingiber	*Phidotricha erigens*
Ziziphus jujuba (see jujube)	

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NOTE

A Checklist of Termites (Isoptera) from Kaieteur National Park, Guyana

Nearly two-thirds of Guyana consists of dense, river-permeated rainforests covering Precambrian rock. On the western border with Venezuela and Brazil, erosion of Roraima sandstone formations, laid down in the Cretaceous, has formed the flat-topped tepuis known as the Pakaraima Mountains. Several rivers begin at the top of the Pakaraimas, in places resulting in spectacular waterfalls. Pedestalled where the Pakaraimas abruptly give way to lowland rainforest, and with a straight drop of 741 ft., Kaieteur Falls on the Potaro River (5°10′N, 59°29′W) is the most dramatic example. It is the second highest waterfall in the Western Hemisphere and is the location of Guyana's only National Park.

A fascinating range of habitats is found in the park. At the top of the falls, and along the upper edges of the canyon lining the Potaro River gorge beyond the falls, water vapor from the roaring tumult wafts over white and pink sand forest adjacent to a shrub-herb savanna. Floral species found there include giant, 3-meter tall bromeliads (*Brocchinia micrantha* [Baker] Mez), bladderworts (*Utricularia humboltii,* Rob. Schomb.), lichens, and numerous trees (Clusiaceae and Rubiaceae families) and shrubs (e.g., *Inga sertulifera* DC.) (Kelloff and Funk 1999. A Checklist of the ferns, fern allies, and flowering plants of Kaieteur National Park, Guyana. Smithsonian Institution, Washington, DC). Many of the trees and are covered with mosses, orchids, and other epiphytes. The Smithsonian Institution's Biodiversity of the Guianas (BDG) Program, in collaboration with the Center for Biodiversity at the University of Guyana, has been conducting a survey of the flora and fauna of the country. As part of an initial BDG expedition to collect and describe the termites of Guyana, we spent four days collecting at Kaieteur National Park. The following report is an annotated checklist of species that were collected, with three sampling areas distinguished: (1) Riverine forest above the falls, (2) white and pink sand forest on the canyon plateau lining the falls, and (3) shrub-herb savanna on the canyon above and beyond the falls. Feeding group assignments follow recent practice (Sleaford et al. 1996. Ecological Entomology, 21: 279–288). Replicate vouchers for these collections have been deposited with the Center for Biodiversity, University of Guyana (Georgetown), The Natural History Museum (London), and the National Museum of Natural History, Smithsonian Institution (Washington, DC). To our knowledge, this is the first survey of termites conducted in Guyana's only national park.

ANNOTATED CHECKLIST

RHINOTERMITIDAE

Dolichorhinotermes longilabius (Emerson). Found with *Araujotermes parvellus* in small branch buried in ground (2); in old dead standing tree stump by river (1); in dead wood (1); wood feeder.

Dolichorhinotermes nr. *tenebrosus* (Emerson). In dead wood (2); in standing wet dead tree stump (2); wood feeder.

Heterotermes tenuis (Hagen). Under bark of dead twig (2); in hard log (2); in carton material at base of rock in sandy soil (3); wood feeder.

Coptotermes testaceus (Linneaus). In rotting log (2); wood feeder.

TERMITIDAE

APICOTERMITINAE

Anoplotermes banksi Emerson. In very humic soil (2); soil feeder.

Anoplotermes genus-group, sp. A. In sandy humic soil under root mass at base of medium-sized tree (2); soil feeder.

Anoplotermes genus-group, sp. B. In suspended soil/roots at base of bromeliad (3); soil feeder.

Anoplotermes genus-group, sp. C. In soil (2); soil feeder.

TERMITINAE

Cylindrotermes parvignathus Emerson. In dry dead wood (2); in very small twigs within root mat of very humic soil (2); wood feeder.

Neocapritermes, n. sp. A. In soil plastered within dead wood (2); soil-wood interface feeders.

Termes fatalis Linneaus. Near river, in carton nest at base of fallen tree (1); soil-wood interface feeder.

NASUTITERMITINAE

Armitermes minutus Emerson. In very decayed wood (2); in root mat within very humic soil (2); in humus-rich root mat at tree base (2); soil-wood interface feeder.

Embiratermes sp. A. In mound on ground (2); soil or soil-wood interface feeder.

Araujotermes parvellus (Silvestri). In dead dry tree stump by river (1); secondary occupant in old *Nasutitermes* sp D carton nest on ground in rocky unforested area, found with *Nasutitermes* sp B (3); in standing dead wet stump (2); with *Dolichorhinotermes longilabius* in small branch (2); in abandoned water-logged carton nest (probably *Nasutitermes*) in very old rotten (but dry) dead tree (2); under bark of dead twig (2). Recorded (Fontes 1982. Revista Brasileira de Entomologia 26: 99–108) in carton nests of other species—it is probably a carton feeder within other termites' nests.

Coatitermes kartaboensis (Emerson). Probably from (2). Reported (Mathews 1977. Studies on termites from Mato Grosso State, Brazil. Academia Brasileira de Ciências, Rio de Janeiro.)[as *Convexitermes* sensu lato] as feeding in rotten dead wood and on material already "transformed" by other termites.

Nasutitermes banksi Emerson. Apparently feeding and nesting on lichen-encrusted rock overlooking the fall (3). However, the mandibular structure and gut contents appear to be typical of *Nasutitermes* species feeding on dead wood. The nesting habit is unusual for the genus.

Nasutitermes intermedius Banks. In dead wood (2); wood feeder.

Nasutitermes gaigei (Emerson). In humic root mass at base of tree (2); wood feeder.

Nasutitermes sp. A. In dry dead wood (2); observed foraging during daytime on forest floor; wood or litter feeder.

Nasutitermes sp. B. Found with *Araujotermes parvellus* in old *Nasutitermes* sp D carton nest on ground (3); wood feeder.

Nasutitermes sp. C. In dead wood (2); wood feeder.

Nasutitermes sp. D. From small low (30–40 cm high) nests on rocky ground (3) and sub-spherical arboreal nests (2); wood or wood/litter feeder.

Emerson (1925. Zoologica, 6, 291–459) recorded 79 species from Guyana, and 89 species are recorded in Araujo (1977. Catalogo dos Isoptera do Novo Mundo. Academia Brasileira de Ciencias, Rio de Janeiro). Clearly, the Kaieteur checklist, with 22 species, does not accurately represent the potential diversity of the Kaieteur area given its habitat diversity. We found a surprisingly high apparent abundance of termites in the humus-rich woodland (area 2) scattered in patches (<1 ha) among the bare areas above the waterfall, although we had too little time to survey the area in detail. The bare areas themselves seem to be devoid of termites except for epigeal nests of *Nasutitermes* sp. D, which may be foraging into the woodland or on dead plant material growing sparsely in the savanna area. Our single observation of *Anoplotermes*-group sp. B in rich suspended humic material at the base of bromeliads suggests, however, that this may be a microhabitat worth investigating in further studies.

The faunistic composition of the area is very similar to that recorded from Kartabo,

suggesting that there was little obvious turnover between the localities. Of the Kaieteur species which were definitely identifiable (i.e., excluding *Nasutitermes, Embiratermes,* and *Anoplotermes* genus-group species to which we were unable to assign species names) only *Termes fatalis, Neocapritermes* n. sp. A, and *Coptotermes testaceus* were not also recorded from Kartabo, and of these the last has been recorded from elsewhere in Guyana (Araujo 1977. Catalogo dos Isoptera do Novo Mundo. Academia Brasileira de Ciencias, Rio de Janeiro). The four *Nasutitermes* to which we have been unable to give species names may or may not fit into existing species concepts; we simply do not have enough specimens to be certain. The *Neocapritermes* species and three *Anoplotermes*-group species appear to be new to science. Taken with samples collected during the same sampling trip in Paruima, Cuyui-Mazuruni, Guyana, 17 new species of *Anoplotermes* were collected in seven days of field work (Davies et al., unpublished data).

In a provisional study of this kind, one might expect to pick up only the most common and widespread taxa. More detailed sampling in the varied habitats of the reserve would undoubtedly reveal numerous other species, some perhaps more characteristic of this unusual habitat.

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NOTE

Otiorhynchus ovatus, O. rugosostriatus, and *O. sulcatus* (Coleoptera: Curculionidae): Exotic Weevils in Natural Communities, Mainly Mid-Appalachian Shale Barrens and Outcrops

The Palearctic, mainly European genus *Otiorhynchus* Germar is represented in North America by 16 adventive species that were introduced, and have been further spread, with shipments of nursery stock or other horticultural products (Warner and Negley. 1976. Proceedings of the Entomological Society of Washington 78: 240–262; Maier. 1978. Environmental Entomology 7: 854–857; Johnson and Lyon. 1988. Insects that Feed on Trees and Shrubs. Cornell University Press, Ithaca, NY, 556 pp.). Several species, including *O. ovatus* (L.), *O. rugosostriatus* (Goeze), and *O. sulcatus* (F.), have become pests of agricultural and horticultural crops (Essig. 1933. California Department of Agriculture Monthly Bulletin 22(7–11): 379–409). Adults are flightless, parthenogenetic, and mainly nocturnal and univoltine. These three species are polyphagous, with larvae generally more host restricted than adults (Smith. 1932. United States Department of Agriculture. Technical Bulletin 325: 1–45; Essig 1933; Warner and

Negley 1976; Nielsen and Dunlap. 1981. Annals of the Entomological Society of America 74: 60–65; Lehman. 1983. Regulatory Horticulture 9(1–2): 19–20; Masaki et al. 1984. Applied Entomology and Zoology 19: 95–106.

Otiorhynchus weevils, now widespread in eastern and western North America, tend to be patchily distributed (Warner and Negley 1976). They are found most often in greenhouses, nurseries, landscape plantings, vineyards, strawberry plantations, and in other agricultural crops (Downes. 1931. Canada Department of Agriculture Pamphlet 5 (n.s.) (2nd rev. ed.): 1–19; Smith 1932; Essig 1933; Warner and Negley 1976; Brandt et al. 1995. Canadian Entomologist 127: 595–604). *Otiorhynchus* species are reported less often from natural communities (Downes 1931) or from wild hosts (Maier 1978; Maier. 1986. Journal of the New York Entomological Society 94: 70–77; Nielsen and Dunlap 1981).

Adults of *Otiorhynchus* species were observed during a study of insects associated with moss phlox in shale barrens and outcrops in the mid-Appalachians (Wheeler. 1995. Virginia Journal of Science 46: 148). Mats of this prostrate phlox were sampled by shaking them over an enamel pan and recording the numbers of *Otiorhynchus* species present. Representative specimens were collected for later confirmation of field identifications. Sampling was conducted mainly from early or mid-April through June 1989–1996 (Wheeler. 1995. Proceedings of the Entomological Society of Washington 97: 435–451). Numbers in parentheses in the following collection records refer to adult weevils observed in the field. Voucher specimens have been deposited in the Cornell University Insect Collection, Ithaca, N.Y.

Otiorhynchus ovatus (L.)

The strawberry root weevil, first recorded in North America from Massachusetts in 1852, now occurs transcontinentally in Canada and the northern United States. Records also are available for many southern states (Warner and Negley 1976). Best known as a pest of strawberry, this species is a generalist that feeds on young conifers and conifer seedlings (Lehman 1983; Brandt et al. 1995). In non-agricultural settings, *O. ovatus* occurs in British Columbia on rocky islands and on mountains up to about 1,220 meters above sea level (Downes 1931).

Collection records.—MARYLAND: Allegany Co., Boy Scout shale barren, Sideling Hill Wildlife Management Area, E. of Little Orleans, 28 May 1996, at base of *Penstemon canescens* (1); Fifteen Mile Creek Rd. at Piclic Rd., Green Ridge State Forest, 23 May 1993, ex *Phlox subulata* (1). MICHIGAN: Marquette Co., sand dunes, Rt. 28 E. of Harvey, 25 July 1991, under *Hudsonia tomentosa* (5). OHIO: Guernsey Co., Twp. Rd. 871, N. of Winterset, 19 May 1991, ex *Phlox subulata* (1). VIRGINIA: Alleghany Co., Rt. 18 nr. Boiling Spring, 14 May 1989, ex *Phlox subulata* (3); Rt. 311 N. of Sweet Chalybeate, 14 May 1989, ex *Phlox subulata* (1); Highland Co., Head Waters shale barren, 2 June (1) and 23 June 1990 (1), ex *Phlox subulata*; Shenandoah Co., Short Mountain shale barren, 4.8 km SE. of Mount Jackson, 11 May 1991, ex *Phlox subulata* (1). WEST VIRGINIA: Greenbrier Co., Kates Mountain shale barren, S. of White Sulphur Springs, 14 May 1989, ex *Phlox subulata* (1); Hardy Co., shale outcrop, Lost River Rd., NW. of Lost River State Park, 5 May 1990, ex *Phlox subulata* (1).

Otiorhynchus rugosostriatus (Goeze)

The rough strawberry root weevil was first reported from North America from the mid-Atlantic states in 1876. It now occurs in British Columbia, Nova Scotia, Ontario, and Quebec, Canada, and in the United States from Rhode Island south to North Carolina and from Washington to Arizona and California. It is an occasional pest of raspberry and strawberry (Essig 1933; Wilcox et al. 1934. Oregon Agricultural Ex-

periment Station Bulletin 330: 1–109; Warner and Negley 1976; McNamara. 1991. *in* Bousquet, Y., ed., Checklist of Beetles of Canada and Alaska. Research Branch Agriculture Canada Publication 1861/E.).

Collection record.—WEST VIRGINIA: Hardy Co., shale outcrop, Lost River Rd., NW. of Lost River State Park, 5 May 1990, ex *Phlox subulata* (1).

Otiorhynchus sulcatus (F.)

The first North American record of *O. sulcatus,* the black vine weevil, was from Massachusetts in the early 1830s. The North American distribution, which is less extensive and more spotty than that of *O. ovatus,* includes Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, and Quebec in Canada, as well as 25 states from Maine to North Carolina and from Alaska to Arizona and California (Warner and Negley 1976; McNamara 1991). The black vine weevil, an important pest of landscape and nursery plants, feeds on more than 150 plant species (Warner and Negley 1976; Masaki et al. 1984; Johnson and Lyon 1988; Lehman. 1989. Regulatory Horticulture 15(1): 17–19). Known wild hosts of *O. sulcatus* are mainly plants near container-grown nursery stock or those in fencerows or woods adjacent to nurseries and suburban landscape plantings (Nielsen and Dunlap 1981; Maier 1986). In British Columbia, Cram and Pearson (1965. Proceedings of the Entomological Society of British Columbia 62: 25–27) found that adult black vine weevils feed on leaves of certain common weeds in peat bogs where blueberries and cranberries are grown.

Collection records.—VIRGINIA: Highland Co., Head Waters shale barren, 26 June 1994, ex *Phlox subulata* (1); Shenandoah Co., Short Mountain shale barren, 4.8 km SE. of Mount Jackson, 14 April 1991, ex *Phlox subulata* (1). WEST VIRGINIA: Greenbrier Co., Kates Mountain shale barren, S. of White Sulphur Springs, 2 June (2) and 23 June 1990 (1), ex *Phlox subulata*; Hampshire Co., shale outcrop, Rt. 50, Shanks, 14 May 1989, ex *Phlox subulata* (3).

Discussion

Some of the shale barrens and outcrops where *Otiorhynchus* weevils were found are near crop fields and major highways. Examples are the Head Waters shale barren near Rt. 250 in Virginia and the shale outcrop along Rt. 50 at Shanks, W. Va. Other collection sites, further removed from highways and agriculture, are less subject to anthropogenic influence; they include the Boy Scout shale barren in Maryland and Virginia's Short Mountain shale barren.

The exotic weevils *O. ovatus* and *O. sulcatus* have colonized shale barrens and shale outcrops of the mid-Appalachians, but the status of *O. rugosostriatus,* encountered only once, is uncertain. *Otiorhynchus ovatus* and *O. sulcatus* adults might use moss phlox for more than shelter. About half of the collections were from shale barrens or outcrops with mats of phlox 1–3 meters from other plant species. It is unlikely that all adults shaken from mats of moss phlox had crawled there after having developed on other host species in shale barrens and outcrops. The black vine weevil adult shaken from moss phlox at the Head Waters shale barren on 26 June 1994 was teneral, suggesting that development had occurred on the plant. In addition, adults of *O. ovatus* were found in Michigan sand dunes under *Hudsonia tomentosa* isolated (>2 m) from other plant species, suggesting that beach-heather serves as a host plant. Roots of moss phlox and other plants that harbored adults of *Otiorhynchus* should be examined for weevil larvae to try to verify a host relationship with these plant species.

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(Cornell University) and R. D. Lehman (Pennsylvania Department of Agriculture) for confirming identifications of *Otiorhynchus* species, and P. H. Adler (Clemson University) for constructive suggestions on an earlier draft of the manuscript. I also thank M. A. Berdine (The Nature Conservancy) for taking me to the Boy Scout shale barren in Maryland.

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NOTE

The Occurrence of *Adicrophleps hitchcocki* Flint (Trichoptera: Brachycentridae) in the Diet of Brook Trout, *Salvelinus fontinalis* Mitchell, in a Small Headwater Stream in Maryland

Analyses of trout diet provide information about water quality and the species and sex ratios of food items. Such studies also support evaluating ecological models of predator-prey relationships and identify taxa important to sustaining growth and reproduction for a particular population of trout. Investigations that span at least a year can provide seasonal information on species being consumed, and thus indicate emergence patterns of the insects on which the trout feed (Elliott. 1967. Journal of Applied Ecology 4: 59–71). Stomach samples of an alpine brook trout population in Wyoming showed that trout feed on the caddisfly, *Glossosoma verdona* Ross, at a minimum of two periods in its life cycle (Duffield et al. 1995. Journal of the Kansas Entomological Society 67: 277–282). The first occurs during the adult emergence and the second occurs when the female caddisflies return to the water to oviposit. Studying another Wyoming stream, Hubert and Rhoades (1989. Hydrobiologia 178: 225–231) showed that brook trout feed on a variety of aquatic organisms from July through September. This diet included the immatures of five families of Trichoptera, with the trout showing preference for Trichoptera larvae as well as beetle larvae. Analysis of the diet samples also showed that aquatic organisms were gradually replaced by terrestrial items as the seasons progressed.

Here we report that the caddisfly, *Adicrophleps hitchcocki* Flint, occurs in the diet of a natural population of brook trout, *Salvelinus fontinalis* Mitchell, in Clifford Branch, a small headwater stream in Frederick County, Maryland. Clifford Branch is a first/second order stream (39°30′N, 77°27′E) which runs southeast from the Catoctin Mountains originating in the Frederick Municipal Forest. It is approximately 1.5 miles long and joins Tuscarora Creek to empty into the Monocacy River. The watershed of Clifford Branch consists of a mixed hardwood forest. The streambed is gravel and small stones. Many of the rocks in the upper reaches are covered with *Fontinalis* sp., an aquatic moss.

Brook trout were caught using artificial flies at various times between 9:00 AM and 7:00 PM, between January 1993, and June 1994. Samples of stomach contents were obtained using a stomach pump as described by Duffield and Nelson (1993. Aquatic Insects 15: 141–148).

Stomach contents from 453 *S. fontinalis* collected at Clifford Branch contained a total of 9,666 items. The total samples obtained per month ranged from 0 (July) to 85 (April), with a mean of 38 (Table 1). The

Table 1. *Adicrophleps hitchcocki* in stomach samples of brook trout from Clifford Branch, Frederick Co., Maryland.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Larvae	22	96	37	3						2	5	19	184
Pharate male				1									1
female				4	22								26
Samples/month	29	60	64	85	44	39	0	23	31	17	34	27	453

number of items per sample ranged from a single specimen in 13 samples to 501 items in a single sample, with an average of 21.3 *Adicrophleps hitchcocki* represented 16% of all Trichoptera recovered and 2% of the total diet items. Only larvae and pharate adults were recovered. Of the 184 larval cases, approximately 25% were empty. A total of 27 pharate adults (26 ♀ and 1 ♂) were obtained. Twenty-six of the pharate adults were recovered in a short seasonal span, on April 24, 1994 or May 1, 1993.

Adicrophleps is a monotypic genus described by Flint (1965. Proceedings of the Entomological Society of Washington 67: 168–176). It is reported to be found in small cool streams in the central eastern North America (Wiggins. 1996. University of Toronto Press, Toronto, 1–457). Glime (1968. Castanea 33: 300–325) contributed much to our knowledge of this species. This diminutive species constructs cases out of pieces of aquatic moss. The small, green, four-sided, tapered cases are quite cryptic, blending into the *Fontinalis*-covered rocks.

This is the first report of *A. hitchcocki* in the diet of trout. *Adicrophleps hitchcocki* was one of the dominant caddisflies recovered in this study, namely 2% of all food items by number and 16% of all Trichoptera. About 87% of the *A. hitchcocki* were larvae, and most of these were consumed in their cases. Most cases recovered from stomach samples were intact, with only a few partially crushed or less than full size.

After the summer, larvae of *A. hitchcocki* were first recovered in the stomach samples in October. Larval representation steadily increased in the samples in the winter months with the peak occurring in February (96 specimens) followed by a gradual decrease. Wiggins (1996) indicated final-instar larvae pupate in May, and first-instar larvae start to appear in July.

While trout may actively forage for the cases, it is more likely that the cases are washed free from the substrate. Increases in the discharge during the winter and early spring months would facilitate this. The brook trout opportunistically feed on these food items in the water column as they pass by their feeding stations.

Tebo and Hassler (1963. Journal of the Elisha Mitchell Scientific Society 79: 44–53) reported the presence of immatures of a number of case-making genera of caddisflies in the diet of trout from streams in western North Carolina. Cased larvae of the genus *Brachycentrus* Curtis (Brachycentridae), were the most abundant insect taken in the bottom samples presumably because of their exposed position in the habitat making them vulnerable to being "grabbed" by foraging trout. This report established that brook trout consume cases made of plant material. *Adicrophleps* and *Brachycentrus* belong to the same family.

Adicrophleps hitchcocki pharate adults were present in stomach samples collected in late April and early May (Table 1), with female specimens predominating. Very few male pharate adults were recovered in stomach samples. The basis for this gender-based dietary selection is unknown. There are no reports suggesting a female-biased sex ratio for *A. hitchcocki*. Our data suggest that *A. hitchcocki* not only has a short emer-

gence period but has only one generation a year.

We assume that the brook trout were feeding on pharate adults as they were rising to the surface to undergo ecolosion. Teneral individuals were most likely intercepted before they could free themselves from the water surface and crawl onto an object out of the water. This obviously is a very vulnerable stage for caddisflies where predators may consume large numbers. Duffield et al. (1995) found the same to be true for the caddisfly, *Glossosoma verdona.*

Within its range, *A. hitchcocki* may actually be a relatively common species in small, cool and unpolluted streams. Good populations have been documented in other streams containing native brook trout populations in both Maryland and Virginia (Duffield 1995, unpublished observations). It is feasible that *A. hitchcocki* is an important dietary item for resident brook trout populations and may play an important role in maintaining their population densities.

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NOTE

Humbugs, Type Specimens, and the Identity of *Asaphocrita pineae* (Amsel 1962), New Combination (Gelechioidea: Coleophoridae: Blastobasinae)

The examination of primary types is an essential part of all taxonomic studies. Type specimens serve as a basis for the original description, the definition for named species, a standard for comparison of specimens of known or unknown identity, and a vehicle for a given name. While early authors (e.g., Linnaeus) did not use types in practice, their necessity subsequently was gradually recognized. Type specimens can be used to settle questions of ambiguity, such as cases of mixed species in the original series. In addition, type specimens may represent a source of data not recorded by the original describer.

Recently, I requested from Staatliches Museum für Naturkunde Karlsruhe, Germany, a loan of the holotype of *Holcocera pineae* Amsel 1962 (Zeitschrift fuer Angewandte Entomologie 49: 392–398) to complete work on a synopsis of the Neotropical Blastobasinae (Coleophoridae). Because museum policy at Karlsruhe restricts the loan of holotypes and allotypes, I was sent a "female" paratype (Fig. 1). Examination of this specimen revealed some very interesting findings—the specimen was a "humbug."

The term "humbug" is familiar to most entomology graduate students. It refers to specimens created by graduate students, usually teaching assistants, for the purpose of testing students on insect morphology and taxonomic identification. Body parts of specimens representing various taxonomic groups are stockpiled and later meticulously selected for the construction of a unique "humbug." These insectan models usually are so painstakingly assembled that they rival Shelley's Frankenstein monster.

The paratype from Karlsruhe was female, but it also was male. The specimen was not

Fig. 1. Paratype, "humbug" specimen, of *Asaphocrita pineae.*

a hermaphrodite nor a gynandromorph. It was a "humbug!" A female metathorax and abdomen, apparently detached as a unit from the anterior portion of the body (as commonly experienced by many microlepidopterists), apparently had been glued mistakenly to the mesothorax of a male specimen, which apparently had lost its posterior part. Further complicating matters, I suspect that the male part is not conspecific with the female part. In fact, the female part is probably that of an undescribed species of Blastobasinae.

Because Amsel figured the genitalia of the male holotype in the original description of *H. pineae,* the identity of this species and it's generic placement are possible. Accordingly, *Holcocera pineae* Amsel is hereby transferred to *Asaphocrita* Meyrick, 1931 **n. comb.** (Exotic Microlepidoptera 4: 33–192), on the basis of the examination of Amsel's drawing of the male genitalia of the holotype. The holotype has a small proximal flange, and the ventral part of valva is greatly narrowed distally as other *Asaphocrita.* However, other generic characters listed for *Asaphocrita* (Adamski and Brown 1989. Mississippi Agricultural Forest Experiment Station Technical Bulletin 165. Mississippi Entomological Museum Publication No. 1, 1–70), cannot be detected unless direct examination of the holotype can be made, or unless a male paratype can be made available for examination. Although I suspect that the female part of the paratype specimen belongs to *Holcocera* Clemens 1863 (Proceedings of the Entomological Society of Philadelphia 2: 119–129), its identity will remain unknown until another female paratype of *A. pineae* is examined or more specimens of this species are collected.

The identity of the female of *A. pineae* appears solvable with the cooperation of curators at Karlsruhe. However, I cannot stop thinking about that obvious glob of glue between the meso- and metathorax of the paratype "humbug" of *A. pineae* in contrast with the lack of adhesive evidence on those humbugs that I had to examine

when taking laboratory examinations in my introductory courses in entomology.

I thank Mr. Guenter Ebert, Landessammlungen für Naturkunde, Karlsruhe, Germany for the loan of specimens, and Carl Hansen of the Office of Imaging, Printing and Photographic Services, Smithsonian Institution, for Fig. 1.

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Note

Dwarf Millipedes (Diplopoda: Polyxenidae) on Pines in an Ornamental Landscape

Polyxenus Latreille (Diplopoda: Polyxenidae) species have been reported to feed on algae in moist leaf litter of broadleaf and pine forests (Hoffman 1990, p. 842. *In* Dindal, ed., Soil Biology Guide. John Wiley & Sons; Nichols and Cooke 1971. The Oxford Book of Invertebrates. Oxford University Press), while other authors consider them "bark dwellers" (Hopkin and Read 1992. The Biology of Millipedes, Oxford University Press). One species, *Polyxenus lagurus* (L.), has been collected from the thatched roof of a vacation home in Germany (Weidner 1974. Praktische-Schadlingsbekampfer 26: 12, 174–176), under stonewalls and in houses (Enghoff 1976. Entomologiske Meddelelser 44: 161–182), and from galls of goldenrod, *Solidago canadensis* L. (Shelley 1988. Canadian Journal of Zoology 66: 1638–1663). In this paper, we report on the occurrence of *Polyxenus lagurus* in still another and distinct habitat, pine trees in ornamental landscapes.

We took beat samples of pine trees and shrubs on 19 June and 27 Aug. 1997 as part of a study to identify predators of pine needle scale (*Chionaspis pinifoliae* (Fitch); Homoptera: Diaspididae). Tree species sampled were preferred hosts of pine needle scale and included *Pinus mugo* Turra (a dwarf cultivar), *P. sylvestris* L. and *P. nigra* Arnold standing within the city limits of Urbana-Champaign, IL. Pines occurred in three types of habitats: 1) "natural areas," park-like habitats wooded primarily with *Pinus* species (n = 24); 2) "grassy areas," dominated by turf that surrounded pine trees (n = 24); and 3) "disturbed areas," pines in ornamental landscape plantings in proximity to paved roads and/or parking lots (n = 25).

We took beat samples from four branches per tree, one at each of the cardinal points, and at mid-canopy. Each branch was beaten four times by a 925 g rubber mallet through approximately a 90° of arc. A 70% ethanol filled enamel pan was held under the branch to capture falling arthropods. All arthropods and debris from a single plant were combined into one sample, and samples were returned to the lab for species separation under a dissecting microscope.

We collected 63 *Polyxenus lagurus* from three of the disturbed habitat sites: plantings between a large parking lot and a busy road in front of a grocery store (n = 61 specimens), in front of a retail store (n = 1), and at the edge of a large parking lot for a shopping mall (n = 1). These three locations were separated by more than 3.5 km. *Polyxenus lagurus* were only collected from trees that supported populations of pine needle scale; however, it seems unlikely that there is any direct ecological relationship between millipedes and the scale insect.

The presence of *Polyxenus lagurus* in beat samples of pines may not be unexpected because Hoffman (1990) reported

that a few species of *Polyxenus* occur in pine forests, especially in the leaf litter, and Hopkin and Read (1992) state that *Polyxenus* are often bark-dwellers. It was surprising, however, that the millipedes were not present in the grassy or natural habitats that were higher in arthropod diversity than the disturbed areas where they were collected (J. F. Tooker, unpublished data). Disturbed areas may provide suitable habitats for *Polyxenus lagurus* because of their dry microclimate (Hopkins and Read 1992) and lower abundance of predaceous arthropods (J. F. Tooker, unpublished data).

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Note

A Type Species Designation for *Actilasioptera* Gagné (Diptera: Cecidomyiidae)

I recently described a new genus named *Actilasioptera* and included in it five new species, all from grey mangrove in Australia (Gagné, R. J. and L. L. Law. 1999. *Actilasioptera* (Diptera: Cecidomyiidae), a new genus for Australasian and Asian gall midges of grey mangroves, *Avicennia* spp. (Avicenniaceae), pp. 22–35. *In* Csóka, G., W. J. Mattson, G. N. Stone, and P. W. Price, eds. The Biology of Gall-Inducing Arthropods. U.S. Department of Agriculture Forest Service General Technical Report NO-199). I neglected to designate a type species there so do so now, viz., *Actilasioptera tumidifolium* Gagné. According to Article 13b of the the International Code of Zoological Nomenclature (Third Edition, 1985), a genus published after 1931 must be accompanied by type fixation. *Actilasioptera* becomes valid as of the date of publication of this note and not the date of its formal description (ICZN).

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Note

Notes on Chilean Orussidae (Hymenoptera) and a Probable New Host Association

Orussidae is the only entomophagous family of Symphyta. Records associate species with wood-boring Coleopotera and Hymenoptera. Middlekauff (1983. Entomology, University of California Publications, Vol. 101, 46 pp.) gave a good summary of known biological information.

Two species of Orussidae have been re-

corded from Chile, *Orusella dentifrons* (Philippi) and *Guiglia chilensis* Benson (Smith. 1988. Systematic Entomology 13: 205–261). Orussids are rarely found, and only several specimens are known for each. Information on host associations is almost entirely lacking for these and for the entire Neotropical fauna of three other genera and 10 species. Thus, clues to possible hosts are significant. A label on a specimen of *O. dentifrons* adult reads *"Nothofagus."* Even though adult collection records are not always accurate, it may have emerged from *Nothofagus* infested by a beetle. An "Orussidae sp." was listed as a parasite of *Oectropsis latifrons* Blanchard (Cerambycidae) by Barriga (1990. Revista Chilena Entomologia 18: 57–59), but we have not located this specimen.

Since 1988, the senior author has examined several more specimens of each species and located the holotype of *O. dentifrons*, and the junior author has discovered some important host information for *G. chilensis*.

Guiglia chilensis.—Smith (1988) saw one specimen, the allotype. The holotype has not been located. The junior author reared one specimen from *Baccharis linearis* (R. and P.) (Compositae), a native plant to Chile and Argentina. Numerous specimens of *Trigonogenium biforme* Cobos (Buprestidae) emerged from stems of the same plant. This buprestid, known only from central Chile, is relatively rare in collections, but, knowing the host plant, it is easy to breed and obtain the adults. A specimen of *G. chilensis* emerged from the buprestid infested stems, and this is the first probable host association for *G. chilensis*. The specimen is from "Chile-R[egión] Metrop[litana], Runge, 18 Oct. 97" and with the additional label "En Baccharis linearis (R. et P.), c/Trigonogenium biforme Cobos." It is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

One other specimen examined by the senior author is labeled "Chile, R. Metrop., El Canelo, 10.Ene.1993, Leg. M. Beéche" (in the Museo Nacional de Historia Natural, Santiago, Chile).

Orusella dentifrons.—Smith (1988) did not locate the holotype. Subsequently, however, the holotype was found at the Museo Nacional de Historia Natural, Santiago, Chile. It bears the following labels "*Oryssus dentifrons*, Los Ulmos. 1864"; "C.U."; "Colección Philippi"; "Holótipo" [red]; "*Oryssus dentifrons* Phil., det Roh. Feb. 1–21"; "Oryssus dentifrons R. R. Philippi det. A. Camousseight"; "Chile M.N.H.N., Tipo No. 110." This agrees with Philippi's description (1873. Stettiner Entomologische Zeitung 34: 296–316). It is undoubtedly the specimen Rohwer (1925. Revista Chilena de Historia Natural 29: 41–46) examined when he redescribed Philippi's types. The condition of the specimen is still essentially as Rohwer stated – the abdomen is missing and the thorax is partially crushed.

Two additional specimens of *O. dentifrons* are labeled as follows: "Fundo Malcho, Linares, Chile, Nov. 1956, L. E. Peña" (in the USNM); "S. Chile, Los Muermos forest, I-19-51, Ross & Michelbacher, collrs." (det. Middlekauff '54) (in the California Insect Survey, University of California, Berkley; W. W. Middlekauff, personal communication).

We thank M. Elgueta for allowing examination of specimens from the Museo Nacional de Historia Natural, Santiago, Chile.

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A NEW SPECIES OF *COELOSTATHMA* CLEMENS (LEPIDOPTERA: TORTRICIDAE) FROM COCOS ISLAND, COSTA RICA, WITH COMMENTS ON THE PHYLOGENETIC SIGNIFICANCE OF ABDOMINAL DORSAL PITS IN SPARGANOTHINI

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Abstract.—The entomofauna of Cocos Island, Costa Rica, includes nearly 100 species of Lepidoptera, among which are 13 species of Tortricidae, most of which are endemic. One of these, ***Coelostathma insularis,*** **new species,** is described and illustrated. The new species is most similar to *C. binotata* (Walsingham) from Mexico among described species. The genus *Coelostathma* Clemens is redescribed, and a lectotype is designated for *C. binotata.* The shared possession of abdominal dorsal pits in *Coelostathma* Clemens, *Amorbia* Clemens, and *Aesicopa* Zeller suggests a close phylogenetic relationship among these genera within Sparganothini; the variably modified subdorsal pits in *Sparganopseustis* Powell and Lambert may or may not be homologous with those of the other genera.

Key Words: Neotropical, endemic species, *Coelostathma insularis, Amorbia,* Archipini, Euliini

Cocos Island is a small volcanic island located in the tropical eastern Pacific, approximately midway between mainland Costa Rica and the Galapagos Archipelago (i.e., ca. 500 km offshore). Its rugged topography and isolation from the mainland have combined to inhibit permanent settlement by humans; consequently, much of the native biota is relatively undisturbed. In 1979 the Costa Rican government designated the island a nature reserve.

The entomofauna of Cocos Island was the subject of an investigation by Hogue and Miller (1981) who cited approximately 75 species of Lepidoptera from the island. Through continued published (e.g., Brown et al. 1991, Brown 1991) and unpublished taxonomic studies, the number of species of Lepidoptera documented from the island has risen to nearly 100. The Tortricidae is well represented on Cocos Island, constituting 13 species (ca. 13% of the fauna), most of which appear to be endemic and undescribed. In this paper we describe one of these as new; two others will be described in a recently completed revision of *Sparganothina* Powell (Landry and Powell 1999). We also comment on the distribution of abdominal dorsal pits within Sparganothini and speculate on the value of these structures as a character for inferring phylogenetic relationships within the tribe.

Materials and Methods

Specimens from Cocos Island were borrowed from the Natural History Museum of Los Angeles County (LACM), Los Angeles, California; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; California Academy of Sciences (CAS), San Francisco, California; and other collections noted in Hogue and Miller (1981). Comparative material was examined at the Essig Museum of Entomology (UCB), University of California, Berkeley; Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; and The Natural History Museum (BMNH), London, England. Dissection methodology follows that summarized in Brown and Powell (1991). Forewing measurements were made with an ocular micrometer mounted in a dissecting microscope. Terminology for wing venation and genitalic structures follows Horak (1984). Abbreviations and symbols are as follows: FW = forewing; HW = hindwing; n = number examined; ca. = circa (approximately); $\bar{x}$ = mean.

Systematics

Coelostathma Clemens 1860

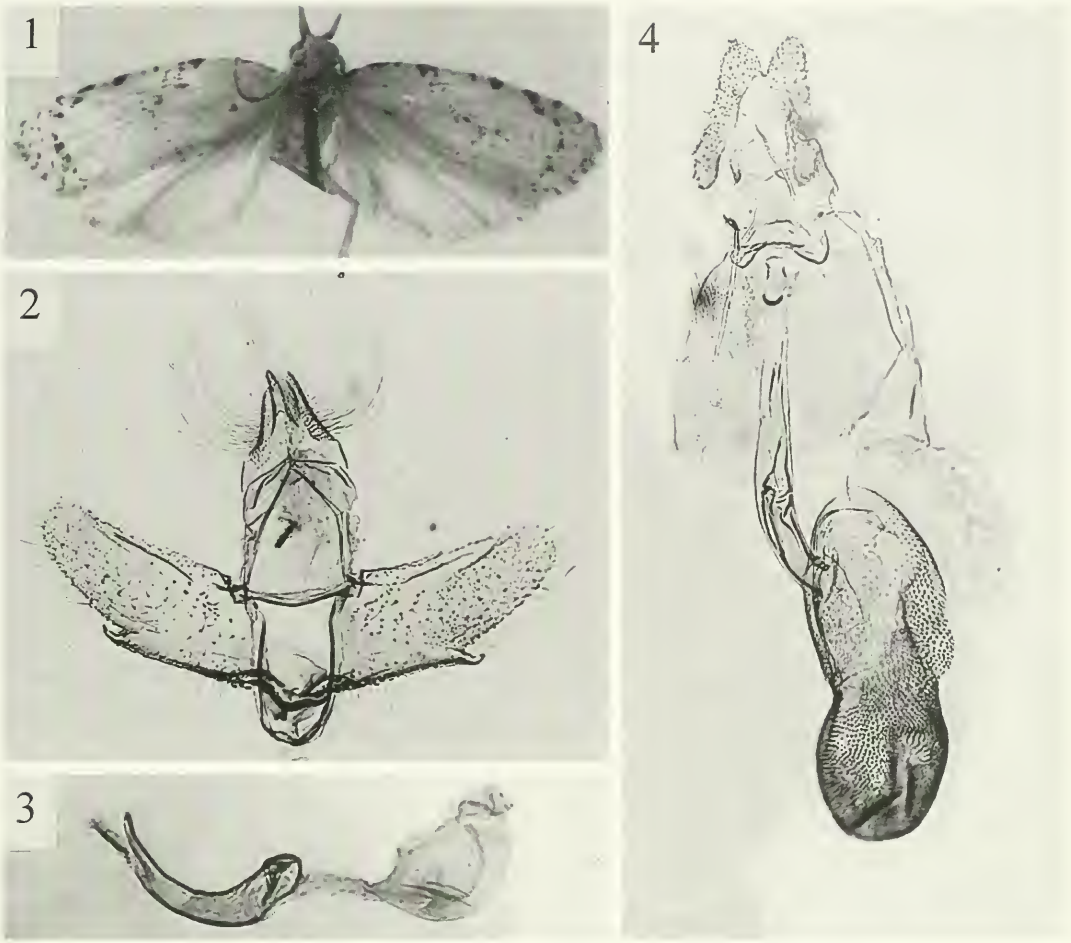
Type species.—*Coelostathma discopunctana* Clemens 1860, by original designation.

Redescription.—*Head:* Antennal scaling in two bands per segment, cilia ca. 1.75–2.25 times flagellomere width in male, short, unmodified in female; ocelli moderate to large; chaetosema present; labial palpus moderately long, upturned, II segment ca. 1.5 times horizontal diameter of compound eye, slightly expanded distally by scaling; III segment 0.2–0.3 as long as II, smooth-scaled, exposed; maxillary palpus rudimentary; proboscis well developed. *Thorax:* Legs unmodified. Forewing length 6–11 mm; apex falcate; costal fold absent in male; upraised scales absent; R_2 and R_3 short-stalked; R_4 and R_5 long-stalked (from $R_2 + R_3$ base). Hindwing with cubital hair pecten well developed in both sexes; no anal fold or hairpencil. *Abdomen:* Usually with a single middorsal pit at anterior edge of A2 (infrequently on other segments as well); female lacking enlarged corethrogyne scaling. Male genitalia with uncus simple, usually slender; socius large, flat, kidney bean-shaped; gnathos absent; transtilla a simple, narrow, spiny band; valva short, somewhat rounded, with attenuate apex; sacculus usually slender, well defined. Aedeagus curved; vesica with patch of slender cornuti. Female genitalia with weakly bilobed sterigma; ductus bursae moderately long, slender, well differentiated from corpus; corpus bursae oblong; signum long, nearly straight (rarely absent). *Sexual dimorphism:* Slight, restricted to subtle differences in color pattern, forewing length (females average slight larger in some species), and antennal cilia length (longer in males).

Coelostathma insularis J. Brown and S. Miller, new species

(Figs. 1–4)

Male.—*Head:* Frons smooth-scaled, white; vertex with overhanging crown of pale tan scales. *Thorax:* Smooth-scaled, pale tan. Forewing (Fig. 1): Length 6.5 mm (n = 1). Pale yellow tan, with pattern elements reduced, comprised of series of small brown dots of variable size, distributed along costa and subterminal region; irregular dotted line from costa ca. 0.75 distance from base to apex, roughly paralleling termen, intersecting dorsum in tornal region. Costal fold absent. Fringe pale yellow tan. Hindwing: Slightly darker than FW ground color; markings absent. Fringe concolorous with HW. *Abdomen:* Single medial dorsal pit on each segment A2–A7. *Genitalia* (Figs. 2, 3): Uncus moderately short, stout, attenuate distally, projecting only slightly beyond dorsal lobe of socius. Socius large, densely scaled, attached subbasally, without



Figs. 1–4. *Coelostathma insularis.* 1, Adult male. 2, Male genitalia, valvae spread. 3, Aedeagus. 4, Female genitalia.

secondary free arms. Transtilla a uniform narrow band, finely spined dorsally. Valva moderately broad, rounded apically; costa differentiated; sacculus well defined, extending ca. 0.6 distance from base to apex, ending in a short, free, curved, pointed tip. Aedeagus (Fig. 3) simple, evenly curved throughout; phallobase simple, rounded; vesica with a bundle of 4–5 slender cornuti.

Female.—FW length 6.5–6.8 mm ($\bar{x}$ = 6.7; n = 2). Essentially the same as male, except antennal cilia ca. 0.1 times width of flagellomere and abdomen with a single medial dorsal pit on A2. *Genitalia* (Fig. 4): Papillae anales simple, slender. Sterigma a lightly sclerotized band with elbowed ventral corners; ring of sclerotization around ostium. Ductus bursae moderately narrow, differentiated from corpus; antrum conspicuous; frail bursa seminalis arising from narrow ductus near antrum. Corpus bursae oblong, densely spiculate; signum absent. Ductus bursae joining corpus subbasally, i.e., approximately 0.7 distance from anterior end.

Types.—*Holotype* ♂*:* COSTA RICA, Cocos Island, Wafer Bay, 17/22 April 1975, C. L. Hogue (LACM). *Paratypes:* Same data as holotype, except collected in forest interior, 1 ♀, 18 September 1984 (T. Werner & T. Sherry, INBio), 1 ♀, 23 September 1984 (T. Werner & T. Sherry, LACM).

Diagnosis.—Adults of *Coelostathma* are characterized by a pale whitish tan ground color with a forewing pattern that usually includes a pair of transverse brown lines or fascia, one in the subterminal region and one across the middle of the forewing, with one or more small, expanded costal patches at the origin of the lines. In *C. insularis* the subterminal line consists of a series of interrupted dashes or dots and is angled rather than curved through the apical region, and the costal patches are extremely reduced. The genitalia of *C. insularis* are most similar to those of *C. binotata* (Walsingham) in the overall shape of the sacculus and valva, and the short uncus in the male, and the subbasal attachment of the ductus to the corpus bursae in the female. Differences in male genitalia between the two are subtle: *C. insularis* has slightly more elongate and attenuate valvae, a shorter uncus (extending only slightly beyond the socius), a more robust and prominent distal termination of the sacculus, and a slightly wider transtilla. In contrast, differences in the female genitalia are striking: in *C. insularis* the portion of the corpus bursae caudad of the attachment with the ductus bursae is uniform rather than narrowed or constricted, and a signum is lacking (all other described species of *Coelostathma* have a well developed, elongate, curved, band-shaped signum).

Most *Coelostathma* have a single middorsal abdominal pit on A2, although these may be variably developed and sometimes difficult to observe in older genitalic preparations. Pits are present on A2 and A3 in *C. parallelana* Walsingham and an undescribed species from Argentina, and absent altogether in an undescribed species from Guatemala and Costa Rica. The single male of *C. insularis* has abdominal pits on A2–A7, the two females on A2.

Distribution and biology.—*Coelostathma insularis* is known only from Cocos Island, Costa Rica. Nothing is known of the biology; consistent with most Sparganothini, the larvae of *Coelostathma* are presumed to be general feeders. See Hogue and Miller (1981) and Brown et. al (1991) for discussion of biogeography and geologic history of Cocos Island.

Etymology.—The species name refers to the insular distribution of this taxon on Cocos Island.

Remarks.—*Coelostathma* Clemens is restricted to the New World, occurring from southeastern Canada (Quebec, Nova Scotia) south through the eastern United States, Central America and the Caribbean, to South America (Colombia, Ecuador, Peru, Argentina). Powell et al. (1995) assigned five species to the genus: *C. binotata, C. contigua* Meyrick (illustrated in Clarke 1958: 90), the type species *C. discopunctana* Clemens, *C. immutabilis* Meyrick (illustrated in Clarke 1958: 90), and *C. parallelana*. Kimball (1965) and Lambert (1950) recognized the presence of an undescribed species in the southeastern United States, and Lambert (1950) recognized four additional undescribed species in the Neotropical Region.

In the original description of *C. binotata,* Walsingham (1914) cited the type series as follows: "*Type* ♂ (66331); ♀ (66332) Mus. Wlsm. (*Godm-Salv. Coll.*) BM. [*PT.* (66338-41, 66345) US. Nat. Mus.]." When both sexes were available Walsingham typically designated a type male and a type female. To alleviate any potential ambiguity, we herein designate the male (66331), from Teapa, Tabasco, Mexico, III-1918, H. H. Smith (BMNH), genitalic slide 7821, as the lectotype of *C. binotata.*

In their revision of *Sparganothina,* Landry and Powell (1999) indicate that the genus may be paraphyletic with regard to *Coelostathma,* and that the latter may not be monophyletic as currently defined. Consequently, the generic assignment of *C. insularis* is provisional pending further analyses of the species of *Coelostathma* (but see discussion below).

Abdominal Dorsal Pits

In a few genera scattered throughout the Tortricinae, the dorsum of abdominal seg-

ments 2–7 of the adult moth possesses rounded, shallowly invaginated cavities that have been referred to as dorsal organs (Diakonoff 1955), abdominal organs (Diakonoff 1955, Varley 1956, Obraztsov 1967), dorsal fovea (Zimmerman 1978), or dorsal pits (Horak 1984). Diakonoff (1954, 1955) discovered these structures in *Tremophora* Diakonoff (Archipini); Varley (1956), Obraztsov (1967), and Razowski (1977) reported them in various species of *Archips* Hübner (Archipini); Obraztsov (1967) reported them in *Amorbia* Clemens and *Coelostathma* Clemens, and incorrectly reported their presence in *Platynota* Clemens (Sparganothini); and Zimmerman (1978) reported them in the pupae of *Panaphelix* Walsingham (Archipini) and *Amorbia.* Horak (1984) summarized these findings, adding *Homona* Walker (Archipini). In some of these genera the number and/or presence of pits varies among species, sexes, and even individuals, shedding doubt on their value in phylogenetic inference.

While the function of dorsal pits is unknown, their homology among apparently disparate genera less than certain, and their presence/absence and/or number variable, these structures still may be valuable indicators of relationships, at least at lower taxonomic levels (e.g., Varley 1956). For example, all species of *Orthocomotis* Clarke and the closely related *Paracomotis* Razowski possess two pairs of pits (located subdorsally), one on A2 and the other on A3 (Brown 1989). All species of *Cuproxena* Powell and Brown possess a single pair of pits (located subdorsally) on A2, and all members of the closely related *Bidorpitia* Brown possess two pairs, one on A2 and one on A3 (Brown and Powell 1991). Although it is highly unlikely that the *Orthocomotis/Paracomotis* group is closely related to the *Cuproxena/Bidorpitia* group, the presence of dorsal pits provides additional evidence for the monophyly of each of these clades. Likewise, Diakonoff (1955) indicated that all species of *Tremophora* possess similar paired dorsal pits in both sexes.

In Sparganothini dorsal pits are present in one or more species of *Coelostathma, Amorbia, Aesiocopa* Zeller, and *Sparganopseustis* Powell and Lambert. Dorsal pits are absent in representatives of all other sparganothine genera we examined (i.e., *Platynota* Clemens, *Niasoma* Busck, *Synalocha* Powell, *Syllonoma* Powell, *Synnoma* Walsingham, *Sparganothis* Hübner, *Paramorbia* Powell and Lambert, *Lambertiodes* Diakonoff, *Sparganothoides* Lambert and Powell, and *Sparganothina* Powell). In *Coelostathma, Amorbia,* and *Aesiocopa,* the pits are single, medial, rounded depressions located at the anterior portion of the abdominal segment, and are present in both sexes. In some specimens the pit(s) appears slightly bilobed, suggesting that it represents the fusion of a pair of adjacent subdorsal pits. When present in *Sparganopseustis* (ca. 50% of species), abdominal pits are paired, subdorsal in position, and conspicuously more developed in males than in females, frequently with modified scaling and/or microtrichia (S. Cho, unpublished). The position and unusual modifications of the pits in *Sparganopseustis* suggest that they may not be homologous with those of other sparganothine genera.

In all North American and many Neotropical *Amorbia* there is a single dorsal pit on A3 (or A2) in both sexes, sometimes with a faint indication of additional pits on A4–A7. In at least some Neotropical species with highly modified labial palpi (e.g., *A. rectilineana* (Zeller)) and/or a large costal fold (e.g., *A. productana* (Walker)), characters which deviate from *Amorbia adumbrana* (the type species) and related species, the pits are absent or inconspicuous. The concordance of these few characters suggests that the presence of dorsal pits may either help define a monophyletic group within *Amorbia* or exclude from the genus those species that lack pits. Alternatively, the pits may have been lost secondarily in the more divergent species.

Although present in nearly all *Coelostathma,* dorsal pits are absent in *Sparganothina,* the putative sister genus (Landry and Powell 1999). As in the examples cited above, dorsal pits may provide convincing evidence for the assignment of species to genera, but may provide no evidence of relationships between or among genera, i.e., the presence of these structures may support the monophyly of *Coelostathma* but provides no evidence of its relationship to *Sparganothina.*

While the presence of dorsal pits in Sparganothini, Archipini, and Euliini may not clarify our knowledge of phylogenetic relationships among these and other tortricine tribes, the structures may prove valuable for assessing relationships within genera and distinguishing between closely related genera. Further investigations into the large array of undescribed Sparganothini may shed additional light (or doubt) on the value of these structures in defining phylogenetic relationships within that tribe.

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A NEW SPECIES OF *MACRUROHELEA* INGRAM AND MACFIE, AND NEW RECORDS OF BITING MIDGES OF THE TRIBES CULICOIDINI AND CERATOPOGONINI (DIPTERA: CERATOPOGONIDAE) FROM TIERRA DEL FUEGO AND THE MAGALLANES

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Abstract.—The first records of biting and predaceous midges of the tribes Culicoidini and Ceratopogonini are provided from Tierra del Fuego and the Magallanes. A new species of predaceous midge, ***Macrurohelea yamana,*** is described and illustrated from Tierra del Fuego, Argentina. *Paradasyhelea brevipalpis* (Ingram and Macfie), *Austrohelea shannoni* (I. and M.), *Stilobezzia (Acanthohelea) varia* I. and M., and *S. (A.) succinea* I. and M., are recorded for the first time from Tierra del Fuego and the Magallanes.

Resúmen.—Se proveen nuevos registros de especies de ceratopogónidos de las tribus Culicoidini y Ceratopogonini para el sector argentino de la isla de Tierra del Fuego, y para islas de la zona de Magallanes en Chile. Se describe e ilustra una especie nueva, ***Macrurohelea yamana,*** de Tierra del Fuego. Se registran por primera vez para el área de referencia a *Paradasyhelea brevipalpis* (Ingram and Macfie), *Austrohelea shannoni* (Ingram and Macfie), *Stilobezzia (Acanthohelea) varia* I. and M., y *S. (A.) succinea* I. and M.

Key Words: Diptera, Ceratopogonidae, Biting midges, new species, Tierra del Fuego, Magallanes

Although 65 species of Ceratopogonidae have been described and/or recorded from Patagonia, only four species are known to occur south of 52°S: *Dasyhelea reynoldsi* Ingram and Macfie (1931), *Forcipomyia wygodzinskyi* Cavalieri (1961a), *F. delpontei* Cavalieri (1961b), and *F. piroskyi* Cavalieri (1961b), all from the large island of Tierra del Fuego. These four species belong to the subfamilies Dasyheleinae (*Dasyhelea*) and Forcipomyinae (*Forcipomyia*) (Borkent and Wirth 1997), but no members of the subfamily Ceratopogoninae have been previously recorded from this region.

Recently, GRS collected specimens of Ceratopogoninae in the tribes Culicoidini and Ceratopogonini from Tierra del Fuego. Additional Malaise trap collections by Dolly Lanfranco during the early 1980's from the Chilean Magallanes of Deceit and Wollaston Islands, that were kindly donated to us by the late W. W. Wirth, prompted detailed examination of all available material from this region. This article presents results of this study, in which we describe and illustrate a new species of *Macrurohelea* Ingram and Macfie, and provide the first records of *Paradasyhelea brevipalpis* (Ingram and Macfie), *Austrohelea shannoni* (I. and M.), *Stilobezzia (Acanthohelea) varia* I.

and M., and *S. (A.) succinea* I. and M., from Tierra del Fuego and the Magallanes. Major collection sites are indicated on the map presented in Fig. 1.

The types of the new species are slide-mounted in Canada balsam, and deposited in the collection of the Museo de La Plata, Argentina. For general ceratopogonid terminology see Downes and Wirth (1981); for terminology dealing with the Ceratopogonini, see Wirth and Grogan (1988).

Tribe Culicoidini

Paradasyhelea brevipalpis (Ingram and Macfie)

Dasyhelea brevipalpis Ingram and Macfie 1931:178 (male; Argentina).

Paradasyhelea brevipalpis: Macfie 1940: 17(combination; generic status); Wirth, 1974:18 (in catalog); Spinelli 1987:667 (female; Argentina, Neuquén and Río Negro provinces); Borkent and Wirth 1997:86 (in catalog).

Distribution.—Argentina, in subantarctic *Nothofagus* forests, from 40°S south to Tierra del Fuego.

New records.—Argentina, Tierra del Fuego, Lake Escondido (50 km NE of Ushuaia), 2-III-1993, G. Spinelli, 1 ♀; Ushuaia, Lapataia Bay, 9/10-I-1995, G. Spinelli, 6 ♀, CDC light trap.

Tribe Ceratopogonini

Austrohelea shannoni (Wirth and Blanton)

Monohelea (Isthmohelea) shannoni Wirth and Blanton 1972:175 (female; Argentina, Bariloche); Wirth 1974:40 (in catalog).

Austrohelea shannoni: Wirth and Grogan 1988:23 (combination; fig. male genitalia); Borkent and Wirth 1997:91 (in catalog).

Distribution.—Argentina, in subantarctic *Nothofagus* forests, from 40°S south to Tierra del Fuego; Chile, Wollaston Island in the Magallanes.

New records.—Argentina, Tierra del Fuego, 10 km W Ushuaia (peat bog) on the route to Lapataia Bay, 1-III-1993, G. Spinelli, 2 ♀; Ushuaia, 1 km N river Tristen, 2-III-1993, G. Spinelli, 1 ♀; 55 km E of Ushuaia, 3-III-1993, G. Spinelli, 1 ♂. Chile, Magallanes, Wollaston Island, Scourfield Bay, 17/25-II-1980, D. Lanfranco, 3 ♂, Malaise trap.

Stilobezzia (Acanthohelea) succinea Ingram and Macfie

Stilobezzia succinea Ingram and Macfie 1931:200 (female, male; Argentina, Bariloche.

Stilobezzia (Neostilobezzia) succinea: Das Gupta and Wirth 1968:142 (in list); Wirth 1974:43 (in catalog).

Stilobezzia (Acanthohelea) succinea: Wirth and Grogan 1988:88; Borkent and Wirth 1997:109 (in catalog).

Distribution.—Argentina, in subantarctic *Nothofagus* forests, from 40°S south to Tierra del Fuego; Chile, Deceit Island in the Magallanes.

New records.—Argentina, Tierra del Fuego, Paso Garibaldi (45 km NE of Ushuaia), 2-III-1993, G. Spinelli, 1 ♂; Ushuaia, Lapataia Bay, 24/28-II-1997, P. Posadas, 1 ♀, Malaise trap. Chile, Magallanes, Wollaston Island, Scourfield Bay, 17/25-II-1980, D. Lanfranco, 8 ♀, Malaise trap; Deceit Island, 19/27-XI-1982, D. Lanfranco, 9 ♀, 13 ♂, Malaise trap.

Stilobezzia (Acanthohelea) varia Ingram and Macfie

Stilobezzia varia Ingram and Macfie, 1931: 191 (female, male; Argentina, Chile).

Stilobezzia (Neostilobezzia) varia: Das Gupta and Wirth 1968:139 (in list); Wirth 1974:44 (in catalog).

Stilobezzia (Acanthohelea) varia: Wirth and Grogan 1988:88; Borkent and Wirth 1997:109 (in catalog).

Distribution.—Argentina, in subantarctic *Nothofagus* forests, from 40°S south to Tierra del Fuego; Chile, environs of Puerto Montt and Chiloe Islands, and Wollaston Island in the Magallanes.

Fig. 1. Map of extreme southern Argentina and Chile, with collection localities indicated on Tierra del Fuego and the Magallanes.

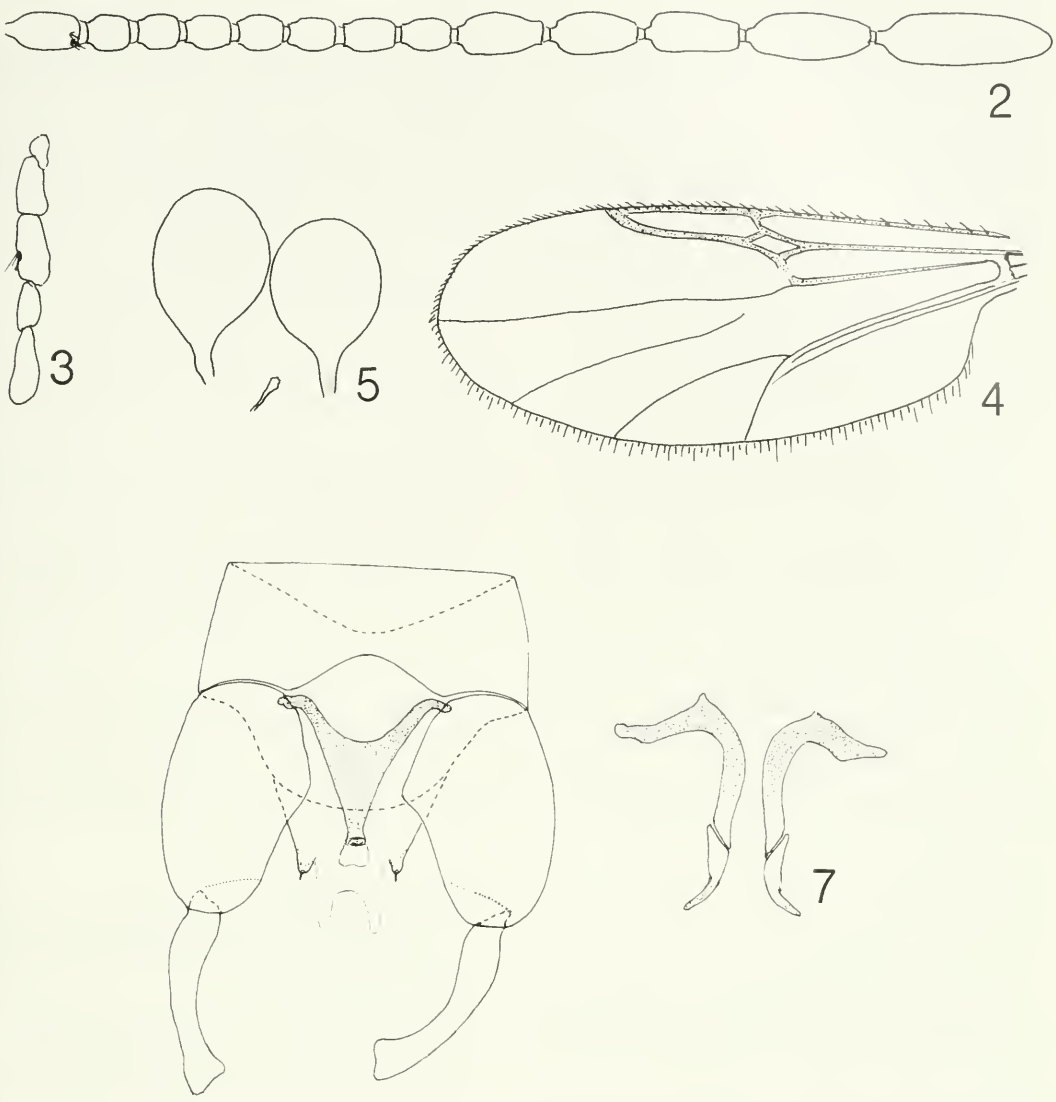
New records.—Argentina, Tierra del Fuego, 12 km W Ushuaia (pond) on the route to Lapataia, 1-III-1993, G. Spinelli, 1 ♀. Chile, Magallanes, Wollaston Island, Scourfield Bay, 17/25-II-1980, D. Lanfranco, 3 ♀, 2 ♂, Malaise trap.

Macrurohelea yamana Spinelli and Grogan, new species

(Figs. 2–7)

Diagnosis.—*Female:* only species in the genus of medium size (wing length 1.50 mm); wing without intercalary vein in cell R5, 2nd radial cell 3× longer than 1st; distal 5 flagellomeres distinctly broader and longer than proximal 8 flagellomeres; and two ovoid spermathecae with long necks. *Male:* only species in the genus having a gonostylus with spatulate tip; cerci finger-like; and the distal portions of the parameres broken at midlength.

Female.—*Head:* Dark brown. Eyes pubescent, separated by distance equal to diameter of 3 ommatidia. Flagellum (Fig. 2) with lengths of flagellomeres (in μm) 52-28-28-32-32-32-32-32-56-56-60-76-108; flagellomeres 9–13 distinctly longer, broader than 1–8; flagellomere 1 with apical sensilla coeloconica; antennal ratio 1.33. Palpus (Fig. 3) with lengths of segments (in



Figs. 2–7. *Macrurohelea yamana.* 2, Female flagellum. 3, Female palpus. 4, Female wing. 5, Spermathecae. 6, Male genitalia, parameres removed. 7, Parameres.

μm) 20-40-44-28-48; segment 3 with very small sensory pit bearing a few capitate sensilla. Mandible with 11 teeth. *Thorax:* Uniformly dark brown; 4 prealar setae, 1 postalar seta; scutellum with 3 large setae. Legs dark brown; hind tibial comb with 6 spines; palisade setae on tarsomere 1 of fore and hind legs; hind tarsal ratio 2.35 (2.30–2.40, n = 2); tarsomeres 4 cordiform; claws small, equal sized, without basal inner teeth. Wing (Fig. 4) with membrane slightly infuscated, anterior veins dark brown, posterior veins light brown; 2nd radial cell 3× longer than 1st; cell R5 without intercalary vein; vein M2 interrupted at extreme base; wing length 1.50 (1.46–1.54, n = 2) mm, breadth 0.65 (0.63–0.67, n = 2) mm; costal ratio 0.71 (0.70–0.72, n = 2). Halter pale brown. *Abdomen:* Brown. Segments 9,10 elongated, bent forward ventrally as is typical for the genus. Spermathecae (Fig. 5) slightly unequal, ovoid with moderately

long necks, measuring 0.053 by 0.038 mm, and 0.045 by 0.038 mm, necks 0.015 mm long.

Holotype male.—Similar to female with usual sexual differences, and following other differences: Wing length 1.48 mm, breadth 0.55 mm; costal ratio 0.66; 2nd radial cell twice as long as 1st. Genitalia as in Figs. 6–7. Sternite 9 moderately long with narrow, shallow caudomedian excavation; tergite 9 moderately short, rounded, apicolateral processes short, nipple-like, each with minute seta; cercus finger-like, pilose. Gonocoxite stout, 1.5× longer than broad with blunt mesobasal protuberance; gonostylus as long as gonocoxite, slightly curved, tip spatulate. Aedeagus heavily sclerotized, narrowly triangular, slightly longer than broad; basal arm short, recurved nearly 90°; basal arch about ¼ of total length; distal portion tapering to moderately broad, blunt, lightly sclerotized tip. Parameres (Fig. 7) separate, heavily sclerotized; basal apodeme elongate laterally; distal portion more lightly sclerotized, broken at midlength, tip recurving slightly ventrolaterally.

Distribution.—Known only from the type-locality on Tierra del Fuego, Argentina.

Type material.—Holotype ♂, Argentina, Tierra del Fuego, Ushuaia, Lapataia bay 24/28-II-1997, P. Posadas, malaise trap; allotype ♀, one paratype ♀, Argentina, Tierra del Fuego, Ushuaia, Los Castores stream, Lapataia Bay, 1-III-1993, G. Spinelli, sweep net.

Etymology.—The specific epithet, a noun in apposition, refers to the Yamana Indians, early inhabitants of Lapataia Bay, the type-locality on Tierra del Fuego.

Discussion.—In the most recent key to Neotropical species in this genus by Spinelli and Grogan (1990), the female of this new species keys to couplet 10, near *M. setosa* Wirth (1965). However, the females of *M. setosa* differ from that of *M. yamana* in being larger (wing length 2.1 mm), the costal ratio is greater (0.81), the legs are covered in bristly setae, the antennal ratio is smaller (1.07), and the spermathecae have short necks.

The male of *M. yamana* keys to couplet 16 near *M. gentilii* Spinelli and Grogan (1984) and *M. irwini* Grogan and Wirth (1980) in the key by Spinelli and Grogan (1990). However, the male of *M. gentilii* differ from the male of *M. yamana* by the gonostylus bent abruptly subapically at more than 90°, the whitish hyaline wing membrane with pale veins, and the distal portions of the parameres not broken at midlength. Males of *M. irwini* differ from those of *M. yamana* in having a gonostylus only half the length of the gonocoxite with a pointed tip, the parameres fused basally and the distal portions are broken at midlength, the aedeagus has a bifid tip, and the greater costal ratio (0.62).

This is the fifteenth species of this genus of Gondawna distribution, 12 species of which are indigenous to southern Argentina and Chile, whereas 3 species inhabit Australia (Lee 1963; Grogan and Wirth 1985).

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ONCOZYGIA CLAVICORNIS STÅL AND *ALLOPODOPS MISSISSIPPIENSIS* HARRIS AND JOHNSTON: ASSOCIATION OF RARELY COLLECTED NEARCTIC TURTLE BUGS (HETEROPTERA: PENTATOMIDAE: PODOPINAE) WITH AN INTRODUCED AFRICAN GRASS

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Abstract.—Adults and nymphs of *Oncozygia clavicornis* Stål were observed in crowns of an African bunchgrass, weeping lovegrass (*Eragrostis curvula* (Schrad.) Nees), at eight sites in Alabama, North Carolina, and South Carolina. Alabama and North Carolina represent new state records, and *E. curvula* is the first host plant associated with this rarely collected turtle bug. Adults overwinter, and two generations apparently are produced on this host. Plant architecture, particularly the dense crowns and vegetative litter that accumulates in crowns of older plants, as well as the loose sandy soils, might have facilitated the colonization of weeping lovegrass by *O. clavicornis*. An adult of another rarely collected turtle bug, *Allopodops mississippiensis* Harris and Johnston, was collected on weeping lovegrass at each of three localities in South Carolina.

Key Words: Insecta, pentatomids, weeping lovegrass, sandhills, host shifts, biodiversity conservation

The pentatomid subfamily Podopinae, containing about 255 species in 64 genera, is distributed nearly worldwide, but attains its greatest diversity in the Ethiopian Region (Barber and Sailer 1953, Schuh and Slater 1995). This group's taxonomic history and relationships within the Pentatomidae and with other Pentatomoidea have been problematic. Two tribes, the Graphosomatini and the Podopini, have been recognized (Schaefer 1981, 1983), but Davidová-Vilímova and Štys (1994) proposed five tribes: Deroploini, Brachycerocorini, and Tarisini in addition to the two previously recognized. A diagnosis of the Podopinae is provided by Rolston and McDonald (1979) and Schuh and Slater (1995). The North American fauna consists of 13 species in six genera, all belonging to the nominate tribe (Froeschner 1988). Several Nearctic genera and species have been described from only one or two specimens (Slater and Baranowski 1970).

Biological information on the Podopinae, often referred to as turtle bugs, is scant. Graphosomatines are associated with dicotyledonous families such as the Apiaceae, Brassicaceae, Chenopodiaceae, and Ranunculaceae, as well as monocots such as grasses. Several Old World species feed on seeds of their hosts. The drably colored Podopini feed mainly on stems of grasses, sedges, or rushes in damp habitats, although few host records are available to discern feeding habits and trends in this tribe (Schaefer 1981, 1983). With the exception of *Amaurochrous cinctipes* (Say) (McPherson and Paskewitz 1984), the habits of North American podopines are largely unknown. Here, I record the colonization of

an introduced African plant, weeping lovegrass (*Eragrostis curvula* (Schrad.) Nees), by *Oncozygia clavicornis* Stål, giving Alabama and North Carolina as new state records. Also reported are three South Carolina collections of another rarely collected Nearctic turtle bug, *Allopodops mississippiensis* Harris and Johnston, from the same plant species.

Oncozygia clavicornis, belonging to a monotypic genus, was described from a specimen from "America borealis, Texas" (Stål 1872); it also has been reported from Florida, Mississippi, Virginia, and South Carolina (Froeschner 1988). A Canadian record (Vancouver, B.C.) probably represents a misidentification (Barber and Sailer 1953, Froeschner 1988). Torre-Bueno (1920) and Blatchley (1926) remarked that this species is rare or very rare whenever found, and most records previous to my study are based on single specimens. Barber and Sailer (1953) in revising the Podopinae (as tribe Podopini of the Graphosomatinae) examined material from seven localities, with the number of specimens not stated, but likely to have been only seven. The National Museum of Natural History, Smithsonian Institution (USNM) has since acquired two additional specimens, one each from Sanford, Fla., and from Folly Beach, S.C. Additional material consists of a specimen from Hurley, Miss. (Mississippi Entomological Museum); two from College Station, Tex. (David A. Rider Collection); and three from Texas (one each from College Station, Lange's Mill [Gillespie Co.], and Minter Springs) and one from Biloxi, Miss. (Texas A&M University Collection). The last-named specimen might be the one Barber and Sailer (1953) mentioned from the Mississippi Agricultural Experiment Station Collection, but which is not now in the Mississippi Entomological Museum (T. L. Schiefer, personal communication). Published bionomical information is limited to the capture of a specimen on a screen trap in a Texas cotton field (Gaines 1933).

Allopodops mississippiensis also belongs to a monotypic genus. Since the description by Harris and Johnston (1936) of a female from Wiggins, Miss., it has been recorded only from two additional localities: Jocassee, S.C., and Falls Church, Va.; both records also are based on single specimens (Barber and Sailer 1953). Three specimens have been added to the USNM since Barber and Sailer's (1953) revision: two from Myrtle Beach, S.C., and one from Santee, S.C. The Falls Church, Va., specimen was collected on a sedge (Cyperaceae) (Hoffman 1971).

Host Plant and Methods

New records of *O. clavicornis* and information on its seasonal history were obtained from 1996 to 1999 during a study of the insect fauna associated with crowns of weeping lovegrass. *Eragrostis curvula sensu lato* is highly polymorphic, its germplasm comprising diverse forms of uncertain taxonomic status. This grass, therefore, is sometimes referred to as the *E. curvula* complex (Gibbs Russell et al. 1991, Burson and Voigt 1996, Poverene and Voigt 1997). Weeping lovegrass, a perennial bunchgrass native to central and southern Africa, is characterized by rapid growth and a dense root system and crown (Crider 1945). It is used for conservation and forage in many (mainly semiarid) regions of the world (Cox et al. 1988, Phillips et al. 1991, Burson and Voigt 1996, Poverene and Voigt 1997). First planted in the United States in Arizona and Oklahoma during the mid-1930s (Crider 1945, Gamble 1970), weeping lovegrass is used along road banks in the southeastern states to reduce erosion (e.g., Richardson and Diseker 1965). It is also used to revegetate mine spoils (Cummings 1947, Tyner et al. 1948, Vogel 1970) and is sometimes planted as an ornamental (Bailey and Bailey 1976, Greenlee 1992). Although *E. curvula* is considered a weed in New South Wales, Australia (Scott and Delfosse 1992), it is not considered invasive in the southern United States (Vogel 1970). The plant, however, is now natural-

ized in Florida and in the southwestern states (Bailey and Bailey 1976).

Southeastern U.S. plantings are of relatively recent origin, the oldest probably dating from the early 1940s. In 1942, the U.S. War Department took over part of the National Wildlife Refuge, McBee, S.C., planting weeping lovegrass in an X pattern in an area cleared as a bombing range (R.P. Ingram, pers. comm.). Most of the plantings, however, have originated since the 1950s or 1960s. Weeping lovegrass was first reported from South Carolina by Radford and Ahles (1959) and from North Carolina by Ahles and Radford (1959), who noted the plant is becoming increasingly abundant in South Carolina. *Eragrostis curvula* was found in only one of 14 counties (Lexington Co., S.C.) during studies of plants in xeric sands of the Fall-line Sandhills (Duke 1961). Weeping lovegrass now occurs in xeric sandhills of all 14 counties that Duke (1961) surveyed in Georgia, North Carolina, and South Carolina in the late 1950s (AGW, personal observation).

Following the discovery of *O. clavicornis* on weeping lovegrass at Fayetteville, N.C., in 1996, I surveyed for the turtle bug in 160 additional plantings of *E. curvula*, mainly along roads in the Fall-line Sandhills (e.g., Duke 1961, Stout and Marion 1993) from North Carolina to Alabama. An axe handle was used to beat the crowns of weeping lovegrass over a white enamel pan. Dislodged adults and nymphs of *O. clavicornis* were recorded, with nymphs mainly identified to stage in the field; representative specimens of adults and nymphs were collected. Adults have been deposited in the USNM.

At irregular intervals, the total numbers of *O. clavicornis* observed were recorded at Fayetteville, N.C., and at three other sites in North Carolina (near Marston) and South Carolina (Middendorf and near McBee); on some of the visits, I also recorded the numbers of plants that yielded adults or nymphs. I made at least one attempt to recollect *O. clavicornis* at those four sites and at two others where it was found—near Pee Dee, S.C., and at Seale, Ala.—to try to verify the establishment of populations on weeping lovegrass. The site in Harnett County, North Carolina, was visited only once, whereas in Richland County, South Carolina, *O. clavicornis* was found only in the fourth season of surveys. Time spent in the field depended on the number of weeping lovegrass plants present, with more time spent sampling at Fayetteville and Middendorf than at the other four sites.

At the North Carolina and South Carolina sites (except nr. Johnsonville, N.C., and nr. Pee Dee, S.C.), I also sampled other grasses, particularly native species, growing within 10 m of weeping lovegrass. The well-developed crowns of bunchgrasses such as broom sedge (*Andropogon virginicus* L.) and wiregrass (*Aristida* spp.) were sampled similarly to those of weeping lovegrass. Grasses with poorly developed crowns that could not be sampled effectively by beating, as well as some *A. virginicus*, were uprooted and the roots shaken over a pan in an attempt to detect podopines.

Results

Oncozygia clavicornis (Fig. 1) was found on weeping lovegrass at eight sites in Alabama, North Carolina, and South Carolina, including Pee Dee, S.C., where the only individual observed was a dead adult. At the other sites (except Harnett Co., N.C., and Richland Co., S.C.), *O. clavicornis* was found during return visits. The numbers of adults and nymphs observed in the field are listed below; the numbers of adults collected and deposited in the USNM are given in parentheses.

ALABAMA: Russell Co., Rt. 431, Seale: 9 Apr. 1997, 2 adults (2); 9 May 1998, 2 adults (1).

NORTH CAROLINA: Cumberland Co., Rt. 401, Fayetteville: 10 July 1996, 4 adults (4), 11 nymphs; 25 Aug. 1996, 17 adults (17), 3 nymphs, 30 of ca. 60 plants positive for *O. clavicornis*; 20 Sept. 1996, 15 adults (2), 2 nymphs, 9 of 20 plants positive; 8

Fig. 1. *Oncozygia clavicornis* on stems of weeping lovegrass, *Eragrostis curvula*.

Mar. 1997, 4 adults, 3 of 30 plants positive; 30 Mar. 1997, 22 adults, 7 of 20 plants positive; 30 Apr. 1997, ca. 40 adults (2), 1 nymph; 12 July 1998, 17 adults (3), 50 nymphs, 16 of 30 plants positive; 6 Sept. 1998, 71 adults (2), 22 nymphs; 5 Dec. 1998, 5 adults (2), 4 of ca. 30 plants positive.

NORTH CAROLINA: Harnett Co., Rts. 24–27, 0.8 km W. of Johnsonville: 31 Oct. 1998, 4 adults (2).

NORTH CAROLINA: Richmond Co., Rt. 1, 2.4 km N. of Marston: 25 Aug. 1996, 9 adults (9), 5 nymphs, 2 of ca. 25 plants positive; 29 Mar. 1997, 1 adult; 12 July 1998, 0 of 25 plants positive.

SOUTH CAROLINA: Chesterfield Co., Rt. 1, 3.9 km N. of McBee: 28 Aug. 1996, 5 adults (5), 2 nymphs, 5 of ca. 20 plants positive; 20 Sept. 1996, 3 adults; 11 July 1998, 1 adult, 1 of 12 plants positive.

SOUTH CAROLINA: Chesterfield Co., Rt. 1, Middendorf: 28 Aug. 1996, 2 adults (2), 1 nymph, 2 of 40 plants positive; 29 Mar. 1997, 3 adults; 15 May 1998, 3 adults (1); 4 June 1998, 2 adults (1); 11 July 1998, 1 adult, 1 nymph, 2 of 50 plants positive; 6 Sept. 1998, 2 adults (1); 5 Dec. 1998, 1 adult, 1 of ca. 40 plants positive.

SOUTH CAROLINA: Marion Co., Rt. 301, 1.8 km N. of Pee Dee: 14 Sept. 1996, 1 adult, dead when found (1); 11 July 1998, 0 of ca. 40 plants positive.

SOUTH CAROLINA: Richland Co., Spears Creek Church Rd., 3.8 km S. of Pontiac, 22 May 1999, 2 adults (2).

In addition to the above records from weeping lovegrass, an adult was beaten from the crown of bushy bluestem (*Andropogon glomeratus* (Walter Britton et al.) in Florida: Polk Co., Rt. 27, 3 km N. of Lake Wales, 17 Mar. 1999.

Allopodops mississippiensis.—Three adults (deposited in USNM) were encountered during surveys of lovegrass in South Carolina. The sites in Pickens County are in the Piedmont rather than Fall-line Sandhills.

SOUTH CAROLINA: Chesterfield Co., Rt. 1, Middendorf, 11 July 1998, 1 adult; Pickens Co., S. of Brookbend Rd. nr. Todds Creek, 3 km S. of Six Mile, 25 Apr. 1997, 1 adult; Glassy Mountain Heritage Preserve, E. of Pickens, 17 Oct. 1998, 1 adult.

Discussion

Native phytophagous insects can rapidly colonize (<100 years) introduced plant species, the new interactions sometimes resulting in partial or complete specialization on the new hosts (Strong et al. 1984, Wheeler and Mengel 1984, Thompson 1994). Since the 1940s, and undoubtedly more recently in some cases, the New World podopine *O. clavicornis* has colonized an African grass, *E. curvula*, in sandhills of the southeastern United States. It is one of the few Nearctic podopines that have been found in dry habitats, most species having been collected in or near marshes, ponds, sloughs, and streams (e.g., Blatchley 1926, Barber and Sailer 1953, Schaefer 1981). *Oncozygia clavicornis* is also known from the Upper Coastal Plain (Pee Dee, S.C.) and Coastal Zone (USNM collection), where it might occur in moister habitats than it does in xeric sandhills. The habitat in which it was found on bushy bluestem in Florida is seasonally wet.

The native host plants of *O. clavicornis* remain unknown; I did not find it on other grasses at sites where it occurred on weeping lovegrass. *Oncozygia clavicornis* might be more difficult to collect on its native hosts than on *E. curvula*, a bunchgrass with a well-developed crown from which podopines can be easily dislodged. The only evidence for a native host association is the collection of an adult on *Aristida* sp. (Poaceae) at Folly Beach, S.C., in November 1944 (USNM collection) and an adult on *Andropogon glomeratus* in Florida (see Results).

More than 125 years after the original description of *O. clavicornis* only about 15–20 specimens have been available in institutional collections. The scarcity of material in collections probably reflects this bug's cryptic or secretive habits, like those of other podopines (Slater and Baranowski 1970, Hoffman 1971), rather than its actual rarity. Several adults I collected from crowns of weeping lovegrass were encrusted with soil, suggesting that this species sometimes occurs on basal stems near ground level or actually enters the soil. Blatchley (1926) mentioned a grayish crust on a Texas specimen of *O. clavicornis*.

When dislodged from crowns of weeping lovegrass, nymphs and adults often were grasping pieces of host stems. They feigned death when disturbed and always moved slowly, such behavior contrasting with that of most other pentatomids. Although *O. clavicornis* appears capable of flight, adults were not observed to fly.

Plant architecture, perhaps more than secondary plant chemistry or other components of nutritional quality, might be key to this podopine's colonization of *E. curvula*. The dense crowns of weeping lovegrass and thick masses of vegetative material that build up around crowns of undisturbed plants (Crider 1945) offer protection from blowing sand, burning, cold, and drought (Phillips et al. 1991), and perhaps natural enemies. In the case of delphacid planthoppers, grasses that produce a consistent thatch not only provide greater refuge from predators, but also more feeding and oviposition sites than thatchless grass species (Denno 1994). I found *O. clavicornis* only on *E. curvula* growing in loose, sandy soils of the Sandhills and Coastal Plain. The bugs were associated with older (unmowed), large plants with accumulated litter except at Fayetteville, N.C., where they also were found on smaller plants lacking a large crown. The structurally complex *E. curvula*, with its dense crown and litter accumulation, might allow *O. clavicornis* to develop greater densities than it can on native hosts of simpler architecture.

Somewhat analogously, the adventive aquatic plant, water hyacinth (*Eichhornia crassipes* (Mart.) Solms), is characterized in

Florida by a rich invertebrate fauna that includes scarce species difficult to find on native hosts such as water lettuce (*Pistia stratiotes* L.). Water hyacinth's three dimensionality probably facilitated its rapid colonization by a diverse community of invertebrates (O'Hara 1967, Carr 1994).

Exotic or nonindigenous plants often affect native biodiversity by altering species composition and disrupting the structure and function of ecosystems (e.g., Vitousek 1986, Greenberg et al. 1997). The planting of Central Asian wheatgrasses (*Agropyron* spp.) in western U.S. rangelands triggered outbreaks of generally innocuous native mirids or plant bugs (Lattin et al. 1994). Establishment of exotic grasses along highways can be detrimental to remnant native vegetation (Milberg and Lamont 1995). The use of African lovegrasses, including Boer lovegrass (*E. curvula* var. *conferta*), to revegetate southwestern U.S. rangelands appears to have adversely affected the native biota (Bock et al. 1986). But in the case of weeping lovegrass in the southeastern United States, its use along roadways might have enabled a scarce turtle to develop larger populations than is possible on native grasses with poorly developed crowns. A subspecies of the dotted skipper (*Hesperius attalus* Edwards) that is rare and local in New Jersey might be adapting to weeping lovegrass in the New Jersey Pine Barrens (Gochfeld 1998).

My observations of *O. clavicornis* populations at irregular intervals allow only tentative conclusions regarding its seasonality. Adults were seen in early December and in early and late March, but nymphs (second or third instar) were not observed until late April, indicating that adults overwinter, as is the case in *Amaurochrous cinctipes* (McPherson 1982). Nymphs of all stages (I–V) were present in mid-July. The presence of late-instar nymphs in early to mid-September suggests that populations are bivoltine rather than univoltine.

Because only three adults of *A. mississippiensis* were found on weeping lovegrass, its status on *E. curvula* is unknown. An *Allopodops* adult was found at Middendorf, S.C., with an adult of *O. clavicornis* and a podopine nymph of apparently the latter species. Further sampling of weeping lovegrass is needed to determine whether *A. mississippiensis* is beginning to adopt this African plant as a host.

Neither *A. mississippiensis* nor *O. clavicornis* might be considered rare under certain criteria (Gaston 1994), but too little is known about their ecological requirements and abundances to assess their rarity or vulnerability. As rarely collected species, they are potentially interesting to conservation biologists. Because both belong to monotypic genera, they are more relevant to the conservation of insect biodiversity than if they were members of species-rich genera.

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DUAL-MIMICRY OF WASPS BY THE NEOTROPICAL LEAFHOPPER *PROPETES SCHMIDTI* MELICHAR WITH A DESCRIPTION OF ITS FEMALE (HEMIPTERA: CICADELLIDAE: CICADELLINAE)

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Abstract.—Diagnostic features of the female of the Neotropical proconiine *Propetes schmidti* Melichar are described and illustrated for the first time. The genus *Propetes* Walker is newly recorded from the State of São Paulo, SE Brazil. The presence of an internal sclerotized plate from abdominal sternite VIII is reported in females of this genus for the first time. The following characteristics of *P. schmidti* suggest that it mimics epiponine wasps (Vespidae: Polistinae): color mostly black in the male and with large yellow areas in the female, pronotum convex, mesoscutellum swollen, forewings hyaline and elongate, and abdomen constricted basally. The different color patterns of males and females suggest a dual, sex-limited Batesian mimicry. This is the first record of mimicry in the tribe Proconiini and of dual-mimicry in an auchenorrhynchan group.

Key Words: Cicadellidae, *Propetes schmidti*, Batesian mimicry, dual-mimicry, Vespidae

Two valid species of the proconiine genus *Propetes* Walker were recorded by Young (1968). *Propetes compressa* Walker, the type species, occurs in northern and central-western Brazil (Pará, Amazonas, and Mato Grosso states) (Walker 1851, Signoret 1855, Melichar 1925, Schmidt 1928, Young 1968). *Propetes schmidti* Melichar is known from central-western Brazil (Mato Grosso do Sul State) (Melichar 1925) and is herein newly recorded from southeastern Brazil (São Paulo State). This genus is closely related to *Homalodisca* Stål (Young 1968), from which it can be distinguished by the following features: (1) head with a median carina on the transition crown-frons; (2) anterior portion of pronotum with a transverse sulcus; (3) scutellum swollen; (4) forewings hyaline; and (5) abdomen constricted basally. The first of these features is apparently a synapomorphy of *P. compressa* and *P. schmidti* (Mejdalani, Takiya and Felix, in preparation). According to Young (1968), *Propetes* is very poorly represented in collections.

In this paper we describe and illustrate the diagnostic features of the female of *P. schmidti* for the first time. Morphological comparisons indicate that *P. schmidti* mimics wasps of the tribe Epiponini (Vespidae: Polistinae). Moreover, the occurrence of a remarkable sexual color dimorphism in this species suggests that males and females mimic different epiponine species. This kind of mimicry, in which each sex has its own model, is called dual-mimicry (Vane-Wright 1976).

Morphological terminology follows mainly Young (1968, 1977), except that of the head, which follows Hamilton (1981).

Techniques for preparation of genital structures follow those of Oman (1949). The dissected parts are stored in microvials with glycerin. Nomenclature of the wasp species follows Richards (1978) with modifications introduced by Carpenter and Day (1988).

Propetes schmidti Melichar
(Figs. 1–7, 9)

Propetes schmidti Melichar 1925: 336; Metcalf 1965: 517; Young 1968: 206.

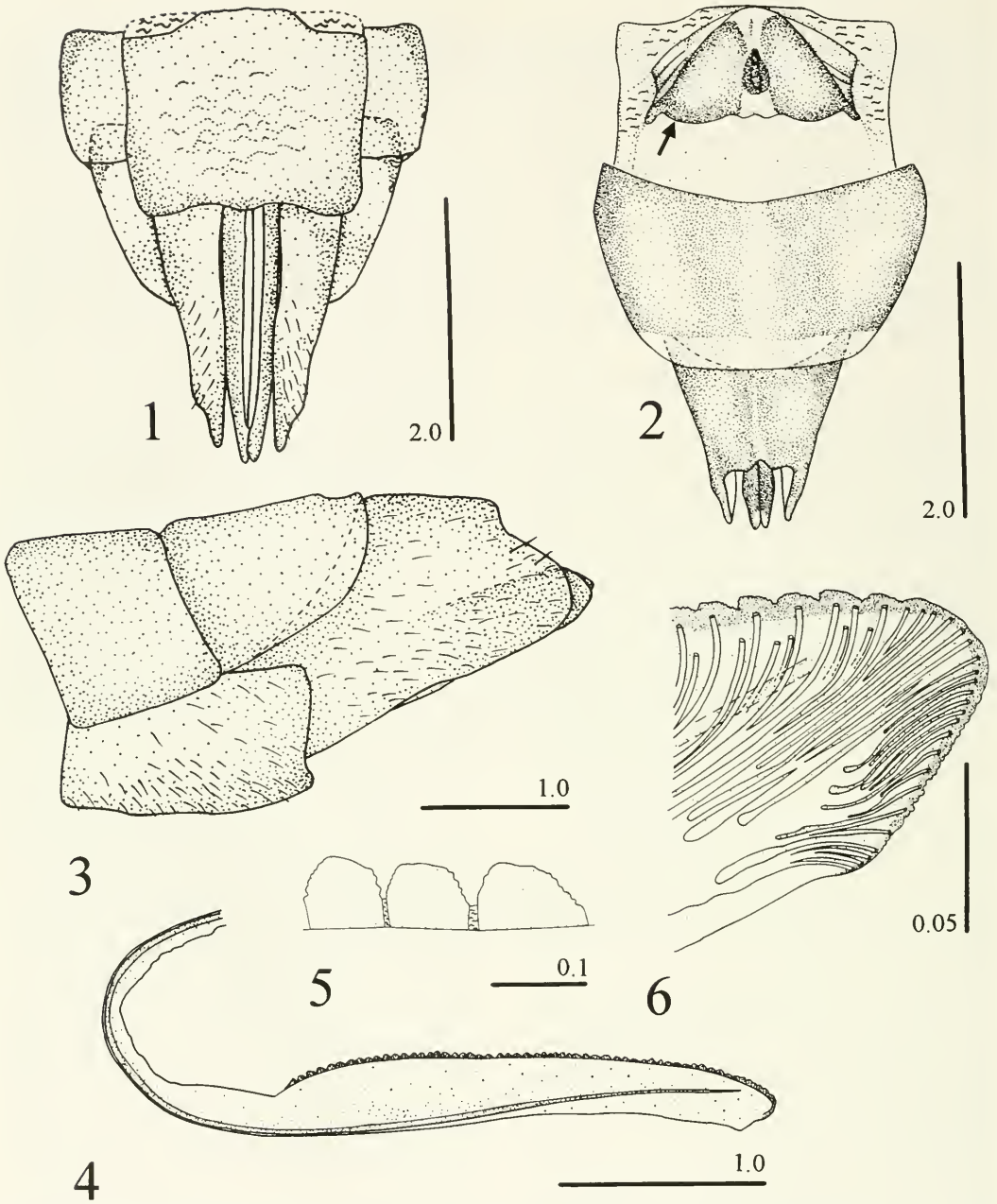
Description.—Length of female 13.2–14.0 mm; male 11.6 mm. Head, prothorax, and mesothorax pubescent. Head (Figs. 7 and 9) strongly produced, median length of crown exceeding interocular width, ocelli located before line between anterior eye angles, genae swollen. Pronotum (Figs. 7 and 9) with anterior transverse sulcus (more conspicuous in female), posterior margin deeply emarginated; mesonotum produced dorsally, lateral margins with strong declivity, scutellum swollen. Forewing (Figs. 7 and 9) hyaline and elongate, anterior portion of costal margin almost straight, exposing posterior meron. Foreleg with tibia expanded near apex. Abdomen (Figs. 7 and 9) constricted basally. Male genitalia, as well as other characteristics of head and thorax, as in the generic description of Young (1968: 204).

Female genitalia: Abdominal sternite VII (Fig. 1) with posterior margin transverse, with small, median blunt projection. Sternite VIII (Fig. 2) in dorsal aspect with two lateral, internal sclerotized plates weakly joined in middle portion, each with oblique fold. Pygofer (Fig. 3) in lateral aspect moderately produced, posterior margin convex, disc with numerous dispersed microsetae and few macrosetae. Second valvulae (Fig. 4) of ovipositor in lateral aspect regularly broadened beyond basal curvature, apex narrowly rounded, preapical prominence not very distinct, blunt, shaft dentate throughout broadened portion, teeth (Fig. 5) subquadrate, becoming gradually smaller, angulate, and more closely spaced toward apex, denticles (Fig. 5) on teeth and ventral margin of shaft before apex (Fig. 6).

Color of female: Crown (Fig. 7) black, with median longitudinal stripe extending from apex to near base, pair of lateral stripes extending from apex to anterior margins of antennal ledges and curved mesally toward ocelli, and marks on antennal ledges and near inner margins of eyes, yellow; frons yellow, with transverse stripe and lateral margins, black; clypeus black, with basal yellow mark; gena yellow; lora brownish or black. Pronotum (Fig. 7) black, with lateral and posterior margins, pair of lateral longitudinal stripes originating from anterior transverse stripe, and median longitudinal stripe originating from posterior margin, yellow; mesonotum (Fig. 7) black, with lateral margins, anterior median stripe, and most of scutellum, yellow. Forewing (Fig. 7) amber. Abdominal tergites (Fig. 7) yellowish brown (or mostly black on tergites VI–IX), posterior margins with transverse brownish marks, tergites III and IV with large yellow marks.

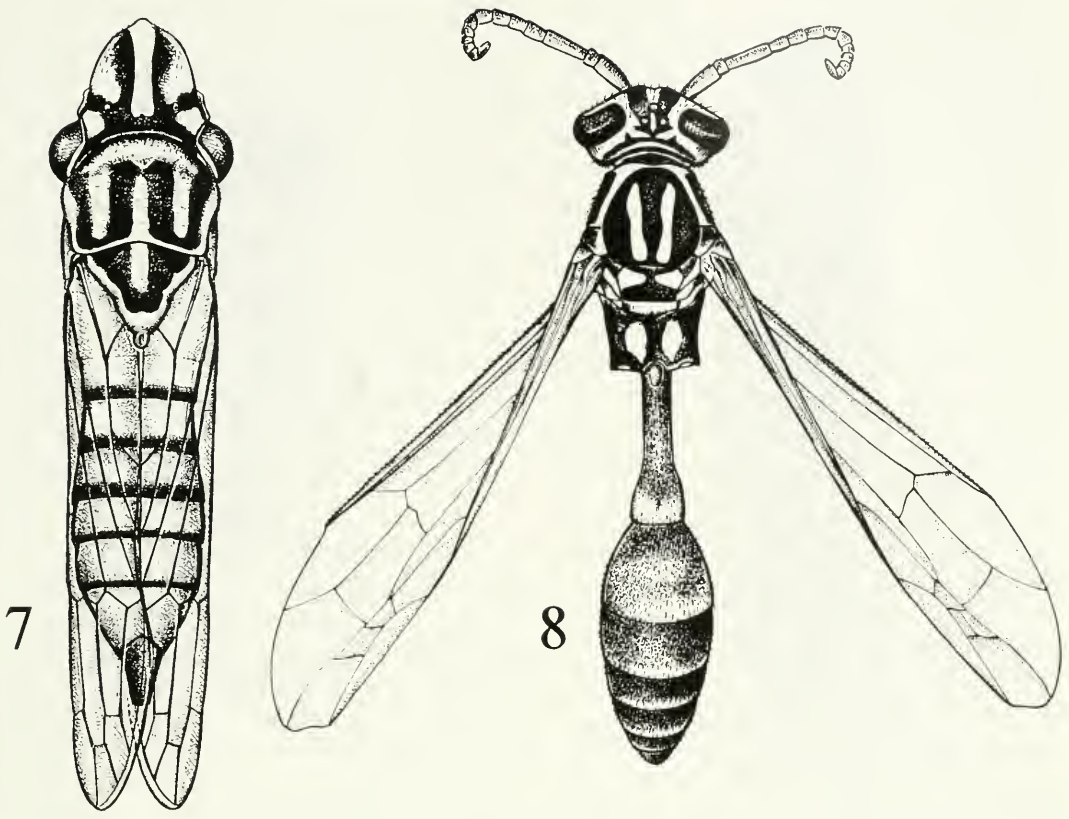
Color of male: Crown (Fig. 9) black, with median longitudinal stripe extending from apex to about line between anterior margins of antennal ledges and marks on antennal ledges and near inner margins of eyes, yellow; frons black, with transverse stripe on superior portion and maculae on inferior portion, yellow; clypeus black; gena black, with yellow macula below antennae; lora black. Pronotum (Fig. 9) black, with lateral and posterior margins and three anterior maculae, yellow; mesonotum (Fig. 9) black, with pair of small anterolateral maculae and macula on posterior half of scutellum, yellow. Forewing (Fig. 9) amber. Abdominal tergites (Fig. 9) black, with yellow maculae.

Material examined [lines on the specimen labels separated by a virgule (/)].—1 ♀ and 2 ♂, "Paulo de Faria-SP [São Paulo State]/ Brasil 10-VII-1996/Yamamoto, P. leg"; 2 ♀, "Bebedouro-SP/Brasil IV-1997/W. Peiffer col."; specimens deposited in the Departamento de Zoologia da Universidade Federal



Figs. 1–6. Genital structures of the female of *Propetes schmidti*. 1–3, Apical abdominal segments. 1, Ventral view. 2, Dorsal view with tergite VII removed (arrow indicating internal sternite VIII). 3, Lateral view. 4–6, Second valvula of ovipositor. 4, General lateral view. 5, Teeth on median portion, lateral view. 6, Detail of apex showing denticles on ventral portion, lateral view. Scales in mm.

do Paraná (Curitiba, Brazil). 1 ♀ and 1 ♂, "Bebedouro-SP-BR [Brazil]/14/mai./1998/ Roberto, S."; specimens deposited in the Departamento de Entomologia da Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo (Piracicaba, Brazil). Paulo de Faria and Bebedouro coordinates are 20°01′51″S 49°23′00″W and

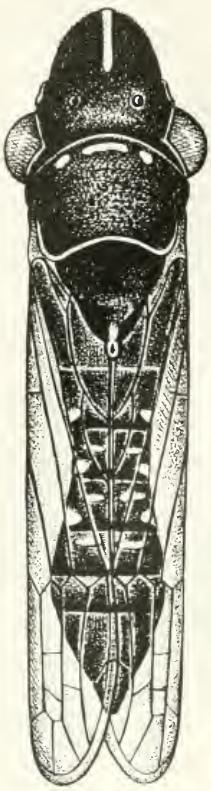


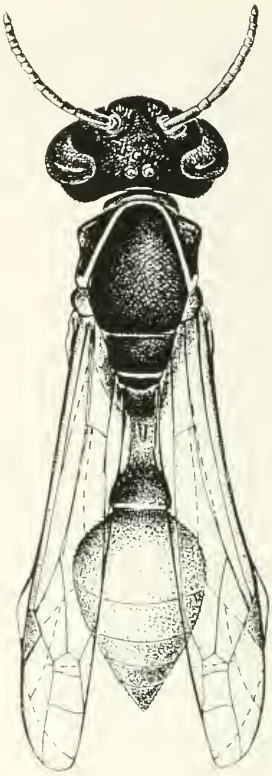
Figs. 7–8. 7, *Propetes schmidti*, dorsal habitus of female, length 13.2 mm. 8, *Myschocyttarus ypiranguensis*, dorsal habitus, a model of the female of *P. schmidti*, length 12.8 mm.

20°56′58″S 48°28′45″W, respectively. This is the first record of the genus *Propetes* from São Paulo State.

Notes.—The male genitalia of the aforementioned specimens of *P. schmidti* agree well with the description and illustrations of Young (1968: 204). As described above, the male color pattern differs remarkably from that of the female. The similar external morphology of both sexes (including specimen size), allied to the collecting data, allowed us to identify them as belonging to the same species. The crown (Figs. 7 and 9) in *P. schmidti* has a longitudinal yellow stripe (longer in the female) that is absent in *P. compressa*, the only other known species of the genus. The female from the former species can be easily identified by the presence of longitudinal and transverse yellow stripes on the pronotal disc (Fig. 7). Unfortunately, the male of *P. compressa* is unknown. The specimens of *P. schmidti* herein described vary in length from 11.6 to 14.0 mm, while specimens identified by previous authors as *P. compressa* are larger, varying from 15 to 18 mm (Signoret 1855, Melichar 1925, Schmidt 1928). The female abdominal sternite VII of *P. schmidti* (Fig. 1) resembles that of *P. compressa*; the posterior margin of this sternite is almost rectilinear in both species.

The presence of an internally well developed sternite VIII (Fig. 2) is here reported in the genus *Propetes* for the first time. Sclerotized internal plates from this sternite were firstly observed by Nielson (1965) in the proconiine genera *Cuerna* Melichar and *Oncometopia* Stål, and later by Mejdalani and Emmrich (1998) in *Dichrophleps* Stål and Mejdalani (1998) in





Figs. 9–10. 9, *Propetes schmidti*, dorsal habitus of male, length 11.6 mm. 10, *Polybia rejecta*, dorsal habitus, a model of the male of *P. schmidti*, length 11.6 mm.

Tretogonia Melichar, *Homoscarta* Melichar, and *Ciccus* Latreille.

One female specimen of *P. schmidti* has a pair of conspicuous, raised rounded chalky blotches on the forewings. These blotches were also observed by Signoret (1855: Pl. XXI, Fig. 9) in *P. compressa* and are found in females of some related genera. They are composed of protein-lipid bodies called brochosomes (R. Rakitov, in litt.; see Rakitov 1995). In *Oncometopia* and *Homalodisca* their formation is related to the preoviposition behavior (Turner and Pollard 1959, Nielson et al. 1975). The presence of these blotches may be a character of generic importance in the Proconiini (Young 1968).

Wasp Models

We studied 10 wasp species belonging to three genera of the tribe Epiponini: *Agelaia cajennensis* (Fabricius), *A. myrmecophila* (Ducke), *A. pallipes* (Olivier), *A. vicina* (de Saussure), *Myschocyttarus parallelogrammus* Zikán, *M. wagneri* (du Buysson), *M. ypiranguensis* da Fonseca (Fig. 8), *Polybia jurinei* de Saussure, *P. quadricincta* de Saussure, and *P. rejecta* (Fabricius) (Fig. 10). The specimens examined are deposited in the Museu Nacional (Rio de Janeiro, Brazil) and were determined by O. W. Richards or J. F. Zikán.

These wasps occur within the geographical range of *P. schmidti* (see Richards 1978). According to their color pattern, they can be easily divided into two groups: (1) species with the head and thorax mostly black; and (2) species with yellow markings on the head and longitudinal yellow stripes on the thorax. The first group includes the wasps belonging to the genus *Polybia* Le-

peletier and the second, to the genera *Myschocyttarus* de Saussure and *Agelaia* Lepeletier. The similarity observed in the color patterns of the species included in each of these groups suggests the existence of two rings of Müllerian mimics. Epiponine wasps often show an aggressive behavior, being mimicked by various insect species. Wasps in the genus *Agelaia*, for instance, are considered as models for some Miridae (Heteroptera), Asilidae and Stratiomyidae (Diptera), and Mantispidae (Neuroptera), as well as for cicadelline leafhoppers in the genus *Lissoscarta* Stål (Richards and Richards 1951, Mejdalani and Felix 1997).

Discussion

Propetes schmidti is approximately the same size as the epiponine wasps. In terms of morphology, the constriction at the base of its abdomen is a remarkable feature. This constriction mimics the petiole at the base of the abdomen of the proposed models. The forewings of *P. schmidti* are elongate and hyaline, resembling those of the wasps. In addition, its convex pronotum and swollen mesoscutellum resemble, respectively, the mesoscutum and mesoscutellum of the wasps. Interestingly, these morphological features (except the swollen scuttellum) are also present in the genus *Lissoscarta* (Boulard 1978, Mejdalani and Felix 1997).

As noted before, there is a remarkable color dimorphism between the female and the male of *P. schmidti*. The former (Fig. 7), which has larger yellow areas and stripes, resembles the epiponines from the genera *Myschocyttarus* (Fig. 8) and *Agelaia*. The latter (Fig. 9), which is mostly black with smaller yellow areas and stripes, resembles the epiponines from the genus *Polybia* (Fig. 10). Therefore, it appears to us that the female and the male of *P. schmidti* each have a different group of Müllerian mimics as models.

According to the terminology and analytic schemes proposed by Vane-Wright (1976), this is a case of Batesian mimicry (class VI, antergic defensive). In addition to the aforementioned morphological and color features of *P. schmidti*, it should be noted that this species is apparently rare (see Young 1968), an aspect that corroborates this hypothesis of mimicry. The predators (operators) from which such mimicry affords protection are unknown. Thus, it is not possible to establish at this time whether this mimicry is disjunct (mimic, model, and operator are different species) or bipolar (model and operator are the same). At least three other cases of class VI mimicry have been reported in the Auchenorrhyncha. One of them is the aforementioned leafhopper genus *Lissoscarta*, which also mimics epiponine wasps. Hogue (1984) suggested that fulgorids in the genus *Fulgora* Linnaeus avoid predation by mimicking arboreal lizards. Zolnerowich (1992) described a fulgorid nymph, *Amycle* sp., that mimics jumping spiders (Salticidae). In the first case Mejdalani and Felix (1997) were also unable to distinguish between the disjunct and bipolar classes of specific composition. In the last two cases the model and operator were considered the same (bipolar).

Vane-Wright (1976) observed that the models in class VI mimicry are often members of Müllerian mimicry groups (class IA, synergic warning). Our conclusion that members of two different color groups of wasps are models for *P. schmidti* is in accordance with his observation. The existence of such distinct models for each sex of *P. schmidti* is a case defined by Vane-Wright (1976) as dual-mimicry. According to that author, this kind of mimicry occurs rarely in Lepidoptera and more commonly in Hymenoptera (e.g., Evans 1968). This is the first report of mimicry in the Proconiini and the first one of dual-mimicry in an auchenorrhynchan group.

Acknowledgments

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STUDIES OF NEOTROPICAL CADDISFLIES LVIII: NEW SPECIES OF THE GENUS *OCHROTRICHIA* MOSELY (TRICHOPTERA: HYDROPTILIDAE) FROM PERU

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Abstract.—Nine new species of the genus *Ochrotrichia* from Peru are described, diagnosed and figured: ***O. intortilis, O. obtecta, O. flexura, O. bipartita, O. calcarata, O. hamatilis, O. machiguenga, O. manuensis,*** and ***O. campanilla.***

Key Words: *Ochtrotrichia,* Trichoptera, Hydroptilidae, caddisfly, new species, Peru

The microcaddisfly genus *Ochrotrichia* Mosely is widely distributed from Canada south through Central and South America as far south as 13°S in central Peru and over the Greater and Lesser Antilles. Four species have been described from Dominican amber (Wells and Wichard 1989, Wichard 1981). A separate subgenus, *Paratrichia,* has been described from Uruguay (Angrisano 1995). Although the first North American species was described in the last century (Hagen 1861), and West Indian and Mexican species in the early part of this century (Mosely 1934, 1937), the first South American species was not made known until 1981 (Flint 1981). This decade has seen 7 more species described from Brazil, Colombia, and Ecuador (Bueno and Santiago 1992). We now add another 9 species from one andean transect, including the Amazonian lowland in Peru. It is clear that many more species remain to be discovered throughout Amazonas and the wetter Andes in South America, perhaps as far south as the Tropic of Capricorn.

The holotypes designated herein are the property of the Museo de Historia Natural "Javier Prado" (MHNJP), Universidad Nacional Mayor de San Marcos, Lima, Peru, but are currently on loan to the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., U.S.A. Paratypes will be divided between MHNJP, NMNH, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), México, and the entomological collection, University of Minnesota, St. Paul (UMSP), U.S.A.

LOCALITIES

This material was collected at only a few localities in Peru in the departments of Cuzco and Madre de Dios. There were two stops on the road between Paucartambo and Pilcopata along the eastern slope of the Andes in a transition area between the andean montane wet forest and andean tropical wet forest. As well, specimens were collected at various sites close to the Pakitza guard station on the banks of the Río Manu in the Manu Reserve Zone of the Manu Biosphere Reserve. The full data for each of these sites is listed below and only an abbreviated citation will be given in the material examined section.

1) Department Cuzco, Province Paucar-

tambo, Puente San Pedro at km 152, 44 km (road) W of Pilcopata, 13°03.30′S, 71°32.78′W, elevation about 1,450 m.

2) Department Cuzco, Province Paucartambo, Quitacalzón at km 164, 32 km (road) W of Pilcopata, 13°01.57′S, 71°29.97′W, elevation about 1,050 m.

3) Department Madre de Dios, Province Manu, Pakitza Posta Vigilante and environs, 65 km (river distance) above Manu, station at 11°56.78′S, 71°17.00′W, elevation 356 m.

Descriptions

Ochrotrichia intortilis Flint and Bueno, new species

(Figs. 1–2)

Ochrotrichia (O.) n. sp. 1: Flint 1996:398.

Diagnosis.—On the basis of the structure of the tenth tergum, i.e, a strong basal spine, a long spine-like process on the right side, and complex central lobe, this species is a member of the *tarsalis* group, most similar to *Ochrotrichia oblongata* Bueno and Santiago (1992). However, *O. intortilis* can be separated from that species by the very heavy, basal spine and the long, curved, right spine that arises basoventrally and the elongate central lobe of tenth tergum.

Adult.—Length of forewing, 3 mm. Color silvery gray; antenna and face with cream-colored hair; forewing silvery gray, with the anterior border covered with a dark band of hair. *Male genitalia:* Ninth tergum capsule like, produced anteriad; sternum with anteroventral angle produced anteriad. Tenth tergum with a single elongate, basodorsal spine to right of midline: right side with a long, slender, twisted spine arising basoventrally; mesally with an elongate, convoluted lobe curved to the left of midline. Inferior appendages long, with a high, basal shoulder, apex rounded; with a row of black, peglike setae along ventral margin and on midbasal ridge, apex with a large cluster of such spines; basoventrally each appendage with a large, pointed lobe produced mesally. Phallus slender, threadlike.

Material.—*Holotype,* ♂*:* PERU; Puente San Pedro, 2–3 Sep. 1988, O. S. Flint & N. Adams (MHNJP). *Paratypes:* Same data, but 24 June 1993, R. Blahnik & M. Pescador, 2 ♂, 1 ♀ (NMNH, UMSP).

Etymology.—From latin: "intortilis," twisted, contorted; in illusion to the tenth tergum.

Ochrotrichia obtecta Flint and Bueno, new species

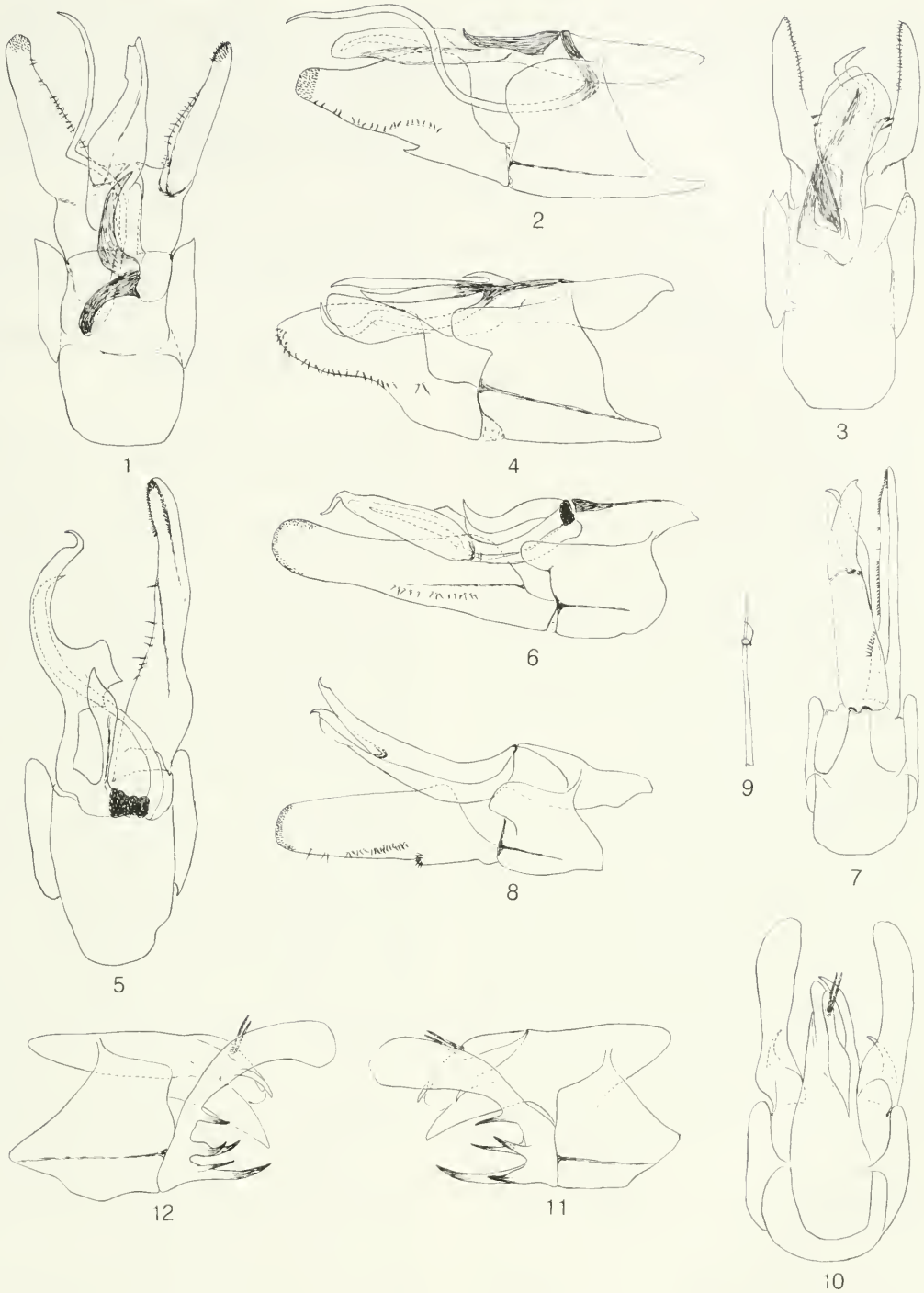
(Figs. 3–4)

Ochrotrichia (O.) n. sp. 2: Flint 1996:398.

Diagnosis.—This species is another member of the *tarsalis* group, as is the preceding species, but very different in the structure of the genitalia. *Ochrotrichia obtecta* is most closely related to *O. tarsalis* (Hagen) (1861) itself, as shown by the apically twisted spine concealed in the tenth tergum. It is easily distinguished from this and all other species by the second strong spine on the right side that is overlain by a thin plate of the tenth tergum.

Adult.—Length of forewing 3 mm. Color silvery gray; antenna and face with cream-colored hair; forewing silvery gray but mostly denuded in type, with the anterior border covered with dark hair. *Male genitalia:* Ninth tergum capsule like, produced anteriad. Tenth tergum with a small basodorsal spine, a long, basolateral spine on right curved to midline and covered by a thin dorsal plate; a long basolateral spine on right curving beneath central complex and ending in a spiral twist; central complex broad and deep, covering both right spines. Inferior appendages long, with a high, basal shoulder, apex rounded; with a row of black, peglike setae along ventral margin and on midbasal ridge, apex with a dense row of such spines. Phallus slender, threadlike, apex slightly enlarged, crescentic.

Material.—*Holotype,* ♂*:* PERU; Puente San Pedro, 2–3 Sep. 1988, O. S. Flint & N.



Figs. 1–12. *Ochrotrichia*. 1–2, *O. intortilis*. 1, Male genitalia, dorsal. 2, Same, right lateral. 3–4, *O. obtecta*. 3, Male genitalia, dorsal. 4, Same, right lateral. 5–6, *O. flexura*. 5, Male genitalia, dorsal. 6, Same, right lateral. 7–9, *O. bipartita*. 7, Male genitalia, dorsal. 8, Same, right lateral. 9, Tip of phallus. 10–12, *O. calcarata*. 10, Male genitalia, dorsal. 11, Same, right lateral. 12, Same, left lateral.

Adams (MHNJP). *Paratypes:* Same data, but 30–31 Aug 1989, N. Adams et al., 1 ♂ (NMNH); same data, but, stream, 3 km E Puente San Pedro, 30 Aug 1998, 1 ♂, 2 ♀ (MHNJP, NMNH).

Etymology.—Derived from latin: "obtecta," covered over; in reference to the spines of the tenth tergum.

Ochrotrichia flexura Flint and Bueno, new species

(Figs. 5–6)

Ochrotrichia (O.) n. sp. 8: Flint 1996:399.

Diagnosis.—On the basis of the presence of several processes of the tenth tergum and by the shape of the inferior appendages, *Ochrotrichia flexura* is considered a member of the *tenanga* group. However, *O. flexura* may be separated from all species, by the processes of the tenth tergum: the large, dorsomesal spine and by the long, curved, left processes enclosed by the right process which is enlarged at midlength and ends in a twisted tip.

Adult.—Length of forewing 2 mm. Color dark brown; antenna and face with cream-colored hair; forewing dark brown with slightly paler markings. *Male genitalia:* Ninth tergum capsule-like, produced anteriad. Tenth tergum in dorsal view, with a large, dorsomesal spine, compressed basally, apically broadened, slightly curved; elongate left process curved to right across midline and slightly recurved to left apicad, enclosed in sheath like right process for apical half; right process narrow basally giving rise to a greatly expanded midsection with apical half curved to left terminating in a hooked apex, internally concave and enclosing left lateral process; basally with a section between mesal and left processes strongly darkened. Inferior appendages symmetrical; in lateral view very long, slender, slightly widened subbasally, apex rounded; apex and ventral margin with a row of black peglike setae. Phallus long and threadlike.

Material.—*Holotype, ♂:* PERU; Pakitza, trail 2, marker 15, Quebrada Trompetero, 6 Jul 1993, R. Blahnik & M. Pescador (MHNJP). *Paratypes:* Same data, 1 ♂ (NMNH); same, but 3 Jul 93, 1 ♂ (UMSP); same, but trail 2, 1st stream, malaise trap, day & night collection, 14–23 Sep 1988, O. Flint & N. Adams, 4 ♂ (MHNJP, NMNH, UMSP).

Etymology.—From the Latin: "flexura," a bending, turning; in reference to the bent apical processes of the tenth tergum.

Ochrotrichia bipartita Flint and Bueno, new species

(Figs. 7–9)

Diagnosis.—*Ochrotrichia bipartita* is clearly a member of the *aldama* group, quite closely related to *O. aldama* Mosely (1937) itself. However, *O. bipartita* can be distinguished from that species by the narrow, elevated, apical section of the ninth tergum, by the longer inferior appendages with a spine bearing lobe on the basal half of the ventral margin, and the details of the shape of the two processes of the tenth tergum.

Adult.—Length of the forewing, 2.5 mm. Color dark brown; antenna cream colored; forewing with a pale, transverse band at midlength and in spots around apex of wing. *Male genitalia:* Ninth tergum encapsulated and produced anteriad, posterior half much narrowed apicad; in lateral view with posterior half strongly elevated apicad. Tenth tergum elongate, divided beyond midlength into two almost equal processes, right process slightly curved left and vice versa and both ending in a small hook. Inferior appendages symmetrical, in lateral view, elongate, apex rounded, at third of length bearing a small, ventromesal lobe with many, black, peglike setae; with a row of black peglike seta around apex, along ventral margin and midbasal ridge. Phallus threadlike, widened basally; subapically with a small, curled spine beyond which extends a slender, straight, short tube.

Material.—*Holotype, ♂:* PERU; stream, 50 m E Quitacalzón, 26 Jul 1993, R. Blahnik & M. Pescador (MHNJP). *Paratypes:* Same data, 5 ♀ (MHNJP, NMNH, UMSP).

Etymology.—From the Latin: "partita," a piece, plus "bi-" prefix for two; in reference to the two parted tenth tergum.

Ochrotrichia calcarata Flint and Bueno, new species
(Figs. 10–12)

Ochrotrichia (O.) n. sp. 3: Flint 1996:398.

Diagnosis.—This is a member of the *arranca* group, very close to *Ochrotrichia yanayacuana* Bueno and Santiago (1992). However, *O. calcarata,* can be separated from that species by the presence of a small spine on the right side of the tenth tergum just above the ventral scoop, and by the size and positions of the basoventral spines on the inferior appendages.

Adult.—Length of forewing 2.5 mm. Color in alcohol dark brown. *Male genitalia:* Ninth tergum capsule like, barely expanded anteriad. Tenth tergum with a slightly curved, dorsal process bearing dorsally two, large, black setae; left side with an slender spine lying along dorsal margin of ventral lobe; ventrally with a scooplike lobe whose tip is pointed in lateral aspect; left side with a slender process apically approximate to central process. Inferior appendages with an elongate clavate dorsal lobe; basoventrally with 5, black-tipped spurs, ventromesal one being longest and arced mesally in ventral aspect. Phallus long, threadlike.

Material.—*Holotype,* ♂*:* PERU; Puente San Pedro, 2–3 Sep. 1988, O. S. Flint & N. Adams (MHNJP).

Etymology.—From the latin: "calcar," a spur; in reference to the spurs from the basal region of the inferior appendages.

Ochrotrichia hamatilis Flint and Bueno, new species
(Figs. 13–14)

Ochrotrichia (O.) n. sp. 6: Flint 1996:398.

Diagnosis.—*Ochrotrichia hamatilis* is considered a member of the *xena* group because of the overall shape of the male genitalia, especially the tenth tergum and inferior appendages, and appears most closely related to *O. gurneyi* Flint (1964). *Ochrotrichia hamatilis* may be distinguished from that species and all others by the shape and structure of the tenth tergum and the presence of a basal hooked appendage on the left inferior appendage.

Adult.—Length of the forewing, 2.5 mm. Color, fuscous; face and antenna with cream-colored hair; forewing fuscous, with a narrow, pale transverse band at midlength. *Male genitalia:* Ninth segment entire with narrow dorsal connection, not produced anteriad; in lateral view almost triangular, posterior margin rounded, not produced. Tenth tergum in dorsal view elongate, asymmetrical, tapering apicad; subapically with a small, right lateral process, tip hooked laterad; ventrobasally with a lightly sclerotized plate, with apical margin sinuate, in lateral aspect with apicoventral angle of this plate pointed ventrad. Inferior appendages in lateral view, elongate, almost parallel-sided, apex rounded; with a row of black peglike seta around apex, along ventral margin and midbasal ridge; left appendage with a hooklike subbasal process, right appendage with only a minute point. Phallus slender, threadlike apicad; constricted subapically with a short point extending from constriction.

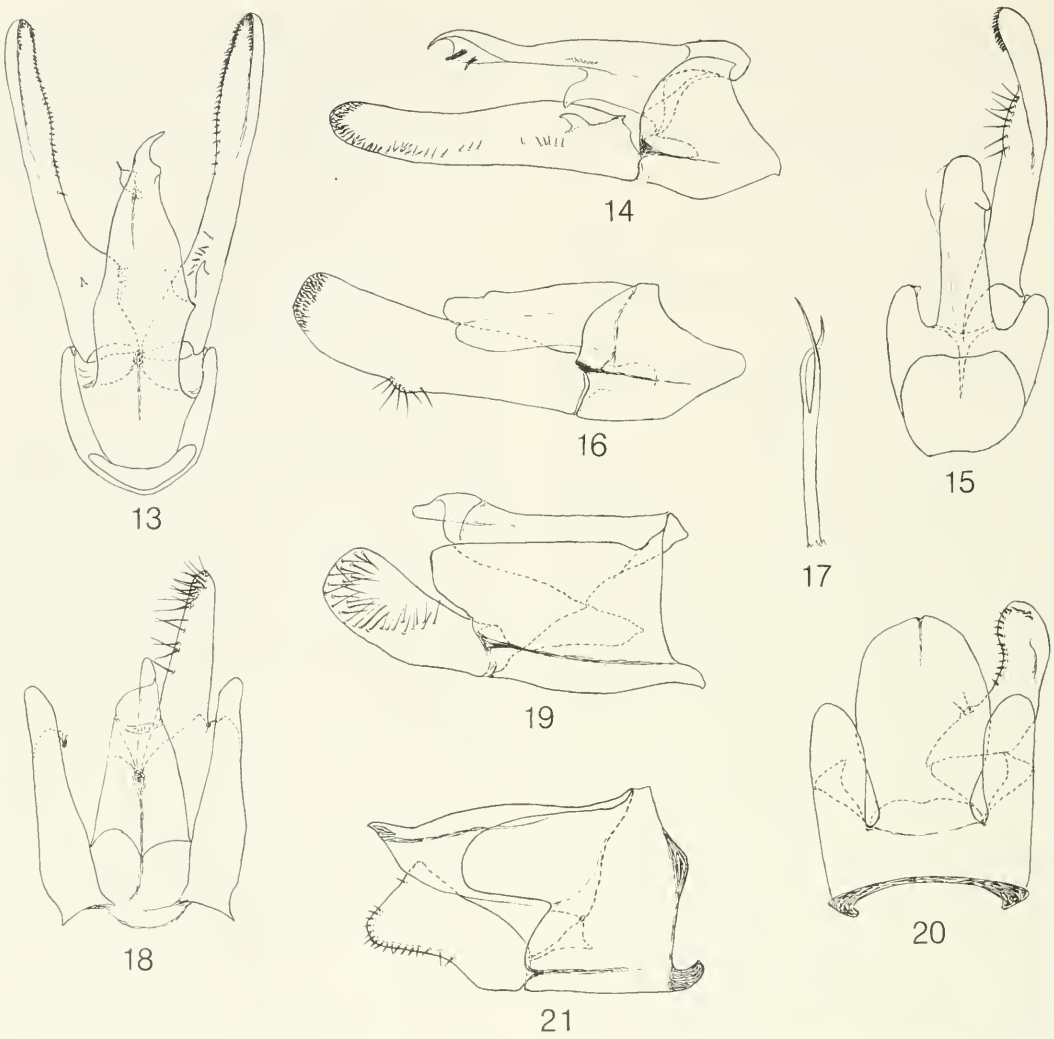
Material.—*Holotype,* ♂*:* PERU; Pakitza, trail 2, first stream, malaise trap, day and night collection, 14–23 Sep 1988, O. Flint & N. Adams (MHNJP). *Paratypes:* Same data, 8 ♀ (MHNJP, NMNH, UMSP).

Etymology.—Latin diminutive of "hamus," a hook or barb; in reference to the apical hook of the tenth tergum.

Ochrotrichia machiguenga Flint and Bueno, new species
(Figs. 15–17)

Ochrotrichia (O.) n. sp. 7: Flint 1996:398.

Diagnosis.—This species is member of the *xena* group that presents some similarities to *Ochrotrichia glabra* Bueno and Santiago (1997). However, *O. machiguenga*



Figs. 13–21. *Ochrotrichia.* 13–14, *O. hamatilis.* 13, Male genitalia, dorsal. 14, Same, right lateral. 15–17, *O. machiguenga.* 15, Male genitalia, dorsal. 16, Same, right lateral. 17, Tip of phallus. 18–19, *O. manuensis.* 18, Male genitalia, dorsal. 19, Same, right lateral. 20–21, *O. campanilla.* 20, Male genitalia, dorsal. 21, Same, right lateral.

can be recognized by the anterior margin of the ninth segment in lateral view being strongly produced at midheight rather than ventrally, and the tenth tergum having a small knob on the left side subapically.

Adult.—Length of forewing, 2 mm. Completely cleared and in alcohol: color unknown. *Male genitalia:* Ninth segment entire, anterior margin produced mesally, tergum continuous. Tenth tergum in dorsal view a simple, elongate, hoodlike lobe, with small knob subapically on left side; in lateral aspect with the apex rounded. Inferior appendages symmetrical; in lateral view parallel-sided, apex rounded; with a cluster of black peglike setae along apex, with several more elongate setae near midbasal ridge which is just beyond midlength. Phallus long, with the apical portion divided into two, slightly curved filaments.

Material.—*Holotype,* ♂*:* PERU; Pakitza, trail 1, marker 14 (1st Stream), malaise trap,

night collection, 19–23 Sep 1989, N. Adams et al. (NMNH).

Etymology.—The name of one of the indian tribes indigenous to the region.

Ochrotrichia manuensis Flint and Bueno, new species
(Figs. 18–19)

Ochrotrichia (O.) n. sp. 5: Flint 1996:398.

Diagnosis.—This species is another member of the *xena* group, clearly related to *Ochrotrichia campanilla* n. sp., *O. flagellata* Flint (1972), and others of the group. It can be distinguished from those species by the much more elongate ninth segment, the odd apical structure of the tenth segment, and in the shape of the inferior appendages, with their much longer than usual spines.

Adult.—Length of forewing, 2 mm. Color dark brown; antenna and face with cream-colored hair; forewing almost uniformly fuscous. *Male genitalia:* Ninth segment entire with narrow dorsal connection, not produced anteriad; in lateral view very long, with small dorsolateral lobe from posterior margin. Tenth tergum an elongate lobe, tapering apicad; apex set-off from basal portion and produced on left side. Inferior appendages in lateral view ellipsoid, apex rounded; with a row of elongate, pointed, black setae around apex, and midbasal ridge. Phallus very long and threadlike.

Material.—*Holotype,* ♂*:* PERU; Pakitza, trail 2, first stream, malaise trap, day and night collection, 14–23 Sep. 1988 O. Flint &. N. Adams (MHNJP). Paratypes: Same data, 1 ♂ (NMNH); same, but night collection, 3 ♂, 4 ♀ (MHNJP, NMNH, UMSP); same, but day collection, 1 ♀ (NMNH); same, but, trail 1, marker 14 (first stream), malaise trap, 19–23 Sep 1989, N. Adams et al., 1 ♂ (NMNH); same, but trail 2, marker 15, Quebrada Trompetero, 6 Jul 1993, R. Blahnik & M. Pescador, 1 ♂, 1 ♀ (NMNH); same, but trail 1, marker 13, Quebrada Paujil-Picoflor, 2 Jul 1993, 1 ♀ (UMSP).

Etymology.—From the locality "Manu," plus Latin suffix "-ensis," inhabitant of.

Ochrotrichia campanilla Flint and Bueno, new species
(Figs. 20–21)

Ochrotrichia (O.) n. sp. 4: Flint 1996:398.

Diagnosis.—This species belongs to the *xena* group, very closely related to the Panamanian *O. flagellata* Flint (1972). From this species, it is easily separated by the much larger dorsolateral lobes from the posterior margin of the ninth segment, the more sharply angled dorsal margin of the inferior appendages, and the lack of the apical appendage on the phallus.

Adult.—Length of forewing, 2 mm. Color dark brown; head and antenna with dark brown hair; forewing mostly denuded but appearing dark brown apparently with some paler maculation, fringe at wing tip with a white spot. *Male genitalia:* Ninth segment entire dorsally, not produced anteriad; with a large dorsolateral lobe from posterior margin. Tenth tergum in dorsal view a large, rounded lobe, with apex bearing a short, dark mark, no spines; in lateral aspect apex produced in an acute, dorsal angle. Inferior appendages in lateral view short, almost bell-shaped, with angulate margin posterodorsally; apical and posteroventral margin with a row of black, peglike setae. Phallus constricted at about 60% of length with both a short pointed process from constriction and a long, slender tubule (possibly with a small point subapically).

Material.—*Holotype,* ♂*:* PERU; Pakitza, trail 1, 1st stream, malaise trap, day collection, 9–14 Sep 1988, O. Flint & N. Adams (MHNJP). Paratypes: Same data, 4 ♂ (IBUNAM, NMNH, UMSP); same, but trail 1, marker 14 (1st stream), malaise trap, night collection, 250 m, 19–23 Sep 1989, N. Adams et al., 1 ♂ (NMNH).

Etymology.—From the Spanish: little bell, "campanilla"; because of the bell-like shape of the inferior appendages in lateral view.

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101(4), 1999, pp. 737–741

FIRST RECORD OF THE PLANT BUG SUBFAMILY PSALLOPINAE (HETEROPTERA: MIRIDAE) FROM JAPAN, WITH DESCRIPTIONS OF THREE NEW SPECIES OF THE GENUS *PSALLOPS* USINGER

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Abstract.—The plant bug subfamily Psallopinae Schuh is reported from Japan for the first time. The discovery also reveals the northernmost distributional record for the subfamily. Three Japanese species of the genus *Psallops* Usinger are described as new: ***P. myiocephalus*, n. sp.**, a temperate zone inhabitant from Honshu and Kyushu, and ***P. nakatanii*, n. sp.** and ***P. yaeyamanus*, n. sp.** from Ishigaki and Iriomote Islands (Yaeyama Group) of the Ryukyus. A key and photographs are provided to distinguish the three Japanese members of *Psallops*.

Key Words: Heteroptera, Miridae, Psallopinae, *Psallops,* new species, Japan

Schuh (1976) established the plant bug subfamily Psallopinae which is currently represented only by five species in two genera, *Psallops grandoculus* Linnavuori and Alamy, *P. oculatus* Usinger, *P. ponapensis* Carvalho, *P. yapensis* Carvalho, and *Isometocoris blantoni* Carvalho and Sailer, and by a Baltic amber fossil, *Isometopsallops schuhi* Herczek and Popov (Schuh 1995). The five modern members are known from Panama, Saudi Arabia and Micronesia.

Recently, I obtained some unique Japanese specimens from my own surveys and from colleagues. These specimens were found to represent three undescribed species belonging to the genus *Psallops,* and they are described below.

All measurements in the text are given in mm. The type specimens are deposited in Biological Laboratory, Hokkaido University of Education, Sapporo, Japan.

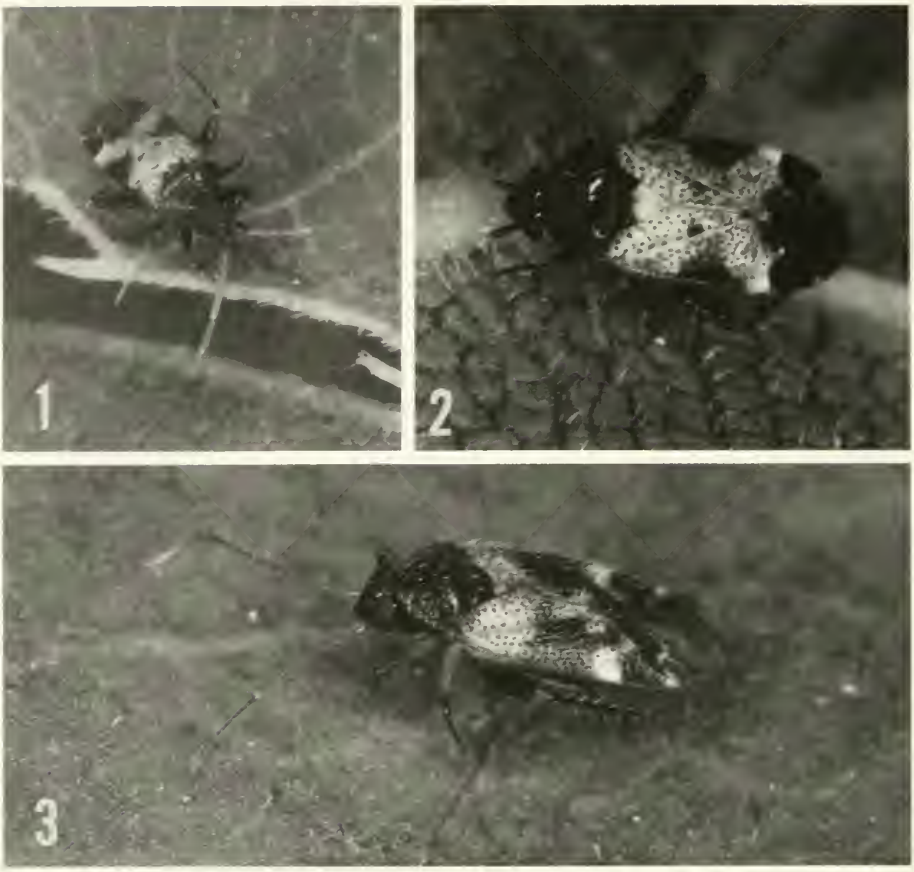
Genus *Psallops* Usinger

Psallops Usinger 1946: 87. Type species: *P. oculatus* Usinger 1946, monotypic.

Usinger (1946) described *Psallops* as a member of the Phylinae, and Schuh (1976) later established the subfamily Psallopinae for it. Subsequently, Henry and Maldonado (1982) reviewed the subfamily to which the Neotropical monotypic genus *Isometocoris* Carvalho and Sailer was transferred from the Isometopinae.

Schuh (1976) indicated that *Psallops* is defined by the finely upturned anterior pronotal margin, 1 or 2 cells on the membrane, 9 metafemoral trichobothria of which 7 are accompanied with the trichomae, 2-segmented tarsi, a subapical tooth of the claw, simple form of the vesica, and phallotheca fused with the phallobase. The Japanese members also possess these characters, except for the vesica with some sclerotized appendages.

In addition to the above characters, the three Japanese species are recognized by the following combination of characters: Body elongate oval; dorsal surface with uniformly distributed, simple, suberect, brown to dark-brown setae; head fuscous,



Figs. 1–3. Adults of *Psallops* spp. 1, *P. myiocephalus*, holotype ♂ on *Quercus acutissima*. 2, *P. nakatanii*, ♀. 3, *P. yaeyamanus*, ♀.

short, subtriangular in dorsal view; eyes enlarged especially in ♂, occupying most part of head, bearing short setae; vertex very narrow, with continuous basal transverse carina; rostrum long, reaching or extending beyond apex of metacoxa; pronotum fuscous, roughened, less than half length of basal width, shallowly and irregularly punctate, somewhat transversely rugose; mesoscutum fuscous; scutellum dark, with more or less pale apex; hemelytra whitish brown, with some dark, symmetrical markings or spots, provided with small, dark, scattered and somewhat convex spots; metafemur fuscous; tibia with long, pale spines; abdomen unicolorously dark brown.

The discovery of a member of *Psallops* in Wakayama Prefecture of Honshu represents the northernmost distributional record for the subfamily.

Psallops myiocephalus Yasunaga, new species

(Figs. 1, 4–8)

Description.— Head with silky, suberect setae, height 0.8 times as width including eyes in frontal view; vertex 0.34 (♂)/1.08 (♀) times as wide as an eye. Antenna dark brown; segment II yellowish or pale reddish brown; lengths of segments I–IV (♂/♀): 0.23/0.26, 0.77/0.76, 0.38/0.46, 0.30/0.33. Rostrum shiny dark brown. Pronotum fuscous, with uniformly distributed, dark, suberect setae; mesoscutum shiny chestnut brown; scutellum dark brown, with at least apical ⅔ whitish; pleura widely reddish

brown, pruinosed; ostiolar peritreme reddish brown. Hemelytra widely whitish brown, with scattered small spots somewhat reddish or sanguineous; corium slightly obscure at inner apical part, mesially with a dark, triangular, large marking continuing to mesial embolium; clavus with an obscure spot mesially; cuneus dark brown, with pale apex in ♀; apex of ♂ left cuneus dark as in Fig. 1; membrane grayish brown. Coxae unicolorously creamy yellow; legs dark brown; basal part of each femur, apical parts of meso- and metatibiae, and all tarsi yellowish brown; lengths of metafemur, tibia and tarsus (♂/♀): 0.86/0.88, 1.44/1.50, 0.35/?. Male genitalia as in Figs. 4–8; vesica with two subapical spines (8).

Dimensions: ♂/♀: Body length 2.5/2.7; head width incl. eyes 0.61/0.57; vertex width 0.09/0.20; mesal pronotal length 0.39/0.38; basal pronotal width 0.88/0.90; width across hemelytra 1.04/1.13.

Holotype.—♂, Konoura, Sotome T., Nagasaki Pref., Kyushu. ex *Quercus acutissima*, 4. viii. 1996, T. Yasunaga.

Paratype.—1 ♀, Wakaura, Wakayama C., Wakayama Pref., Honshu. 25. viii. 1991. M. Kitabata.

Etymology.—From the Greek, myia (= fly) in combination with cephalus (kephalos) (= head), referred to the fly-like head of this new species.

Remarks.—Resembling *Psallops oculatus* Carvalho, the present new species is easily distinguished by the different coloration on the scutellum and hemelytra (see Carvalho, 1956).

I collected a male of *P. myiocephalus* from an oak, *Quercus acutissima* (Fagaceae) in Nagasaki Prefecture of Kyushu. This is the only species of *Psallops* known from a temperate zone.

Psallops nakatanii Yasunaga, new species

(Figs. 2, 9–10)

Description.—Head shagreened, with silky, upright pubescence, height 0.69 as long as width including eyes in frontal view; vertex 0.28 (♂)/1.13 (♀) as wide as an eye. Antenna reddish brown, except for segment I infuscate; lengths of segments I–IV (♂/♀): 0.23/0.24, 0.84/0.75, 0.19/0.36, 0.24/0.28. Rostrum shiny brown; segment I dark brown; scutellum sanguineous anteromesally, with apical ⅔ whitish brown; pleura widely reddish brown, with ostiolar peritreme yellow. Clavus with a distinct dark mesial spot and extreme apex infuscated; semi-circular large mesial marking of corium continuing to embolium; dark, inner apical marking of corium distinct; membrane somber grayish brown. Coxae pale brown; legs dark brown, partly tinged with red; pro- and mesofemora yellow basally; apical parts of tibiae and whole tarsi yellowish brown; lengths of metafemur, tibia and tarsus (♂/♀): 0.96/0.88,? /1.44,? /0.29. Male genitalia as in Figs. 9–10; vesical spines long and slender (10).

Dimensions: ♂/♀: Body length 2.8/2.4–2.9, head width 0.68/0.60–0.62, vertex width 0.08/0.22–0.23, mesal pronotal length 0.41/0.40, basal pronotal width 0.92/0.96–0.99, and width across hemelytra 1.08/1.12–1.17.

Holotype.—♂, Funaura, Iriomote Is., Yaeyama Group, Ryukyus, light trap. 10. v. 1993. Y. Nakatani.

Paratypes.—1 ♀. Omoto, Ishigaki Is., Yaeyama Group, Ryukyus, light trap, 21. v. 1998, K. Takahashi; 1 ♀, Sakae, Ishigaki Is., 27. iii. 1999, K. Takahashi.

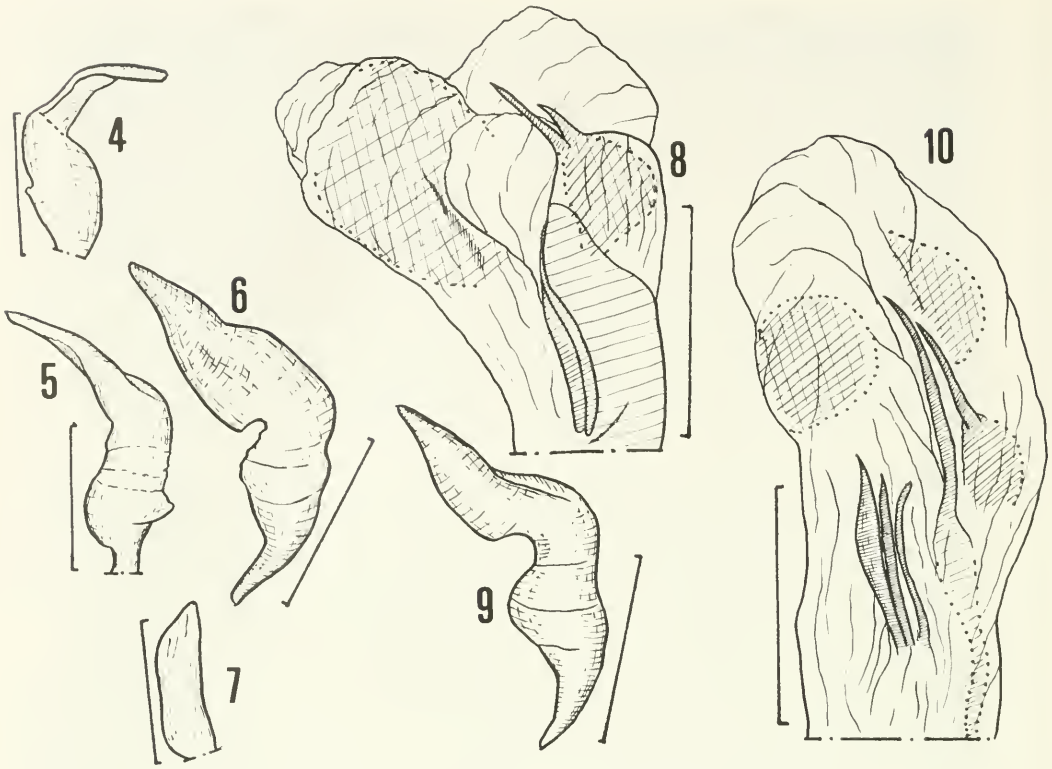
Etymology.—Named after Dr. Yukinobu Nakatani, who collected and offered me the holotype specimen.

Remarks.—This new species is closely allied to the preceding one, from which it can be distinguished by the characters in the key and different structure of the male genitalia.

Psallops yaeyamanus Yasunaga, new species

(Fig. 3)

Description.—*Female:* Dorsal surface with pale vestiture, lacking darkened setae. Head with silvery, suberect pubescence,



Figs. 4–10. Male genitalia of *Psallops myiocephalus* (4–8) and *P. nakatanii* (9–10). 4–6, 9, Left paramere. 7, Right paramere. 8, 10, Vesica. Scales: lines = 0.1 mm.

height 0.86 times as long as width including eyes in frontal view; vertex 0.84–0.91 times as wide as an eye. Antenna pale brown; segments III and IV dark brown; lengths of segments I–IV: 0.24–0.27, 0.88–0.93, 0.48–0.50, 0.32–0.36. Pronotal setae pale brown; mesoscutum shagreened; apical ⅓–½ of scutellum yellow; pleura widely reddish brown, with yellow ostiolar peritreme. Hemelytra with dark, wide marking forming almost continuous U- or W-shaped fascia posteriorly (Fig. 3); cuneus, except for yellow extreme apex, dark brown; membrane pale grayish brown. Coxae and legs yellowish brown; apex of each femur sanguineous; metafemur dark brown; basal half of metatibia darkened; lengths of metafemur, tibia and tarsus: 1.08–1.12, 1.76–1.80, 0.34–0.36. *Male:* Unknown.

Dimensions: ♀: Body length 2.9–3.3; head width incl. eyes 0.63–0.65; vertex width 0.19–0.20; mesal pronotal length 0.47–0.48; basal pronotal width 1.00–1.06; width across hemelytra 1.28–1.32.

Holotype.—♀, Mt. Uehara, Iriomote Is., Ryukyus, 12. v. 1993, T. Yasunaga.

Paratypes.—Ryukyus, Yaeyama Group: 1 ♀, Omoto, Ishigaki Is., 9. v. 1993, T. Yasunaga; 1 ♀, same locality, light trap, M. Tomokuni; 1 ♀, Takeda, Ishigaki Is., 27. xi. 1998, K. Takahashi; 1 ♀, Mt. Buzama, Ishigaki Is., 16. iv. 1998, K. Takahashi; 1 ♀, same locality, 13. xii. 1998, K. Takahashi; 1 ♀, Komi, Iriomote Is., 13. v. 1993, T. Yasunaga.

Etymology.—Named after the Yaeyama Group of the Ryukyus, type locality of this new species.

Remarks.—This new species is easily distinguished from *P. myiocephalus* and *P.*

nakatanii by the generally larger size, pale setae on the dorsum, and the widely infuscated hemelytra.

Psallops yaeyamanus was collected by sweeping broad-leaved evergreen trees, and by a light trap.

Key to Japanese Species of *Psallops*

1. Antennal segment I pale brown; setae on pronotum pale; scutellum pale on apical ⅓–½; dark maculation on hemelytra large, forming an almost continuous fascia (Fig. 3) . . . . . *yaeyamanus*
– Antennal segment I fuscous; pronotal setae dark; more than apical ⅔ of scutellum pale; dark markings on hemelytra symmetrically divided to each side 2
2. Mesial dark marking on corium to embolium triangular; dark spots on inner apical part of corium and mesial part of clavus obscure; apex of clavus pale (Fig. 1) . . . . . *myiocephalus*
– Mesial dark marking on corium to embolium semi-circular, dark spots on inner apical part of corium and mesial clavus distinctly fuscous; apex of clavus infuscated (Fig. 2) . . . . *nakatanii*

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA VICINA* (WULP) (DIPTERA: TEPHRITIDAE) ON WILD AND CULTIVATED ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea vicina* (Wulp) is a multivoltine, narrowly oligophagous fruit fly (Diptera: Tephritidae) mainly infesting flower heads from at least four genera of Asteraceae in the subtribe Pectidinae of the tribe Helenieae, including cultivated marigold (*Tagetes* sp.), in the southwestern United States. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The egg pedicel has a single row of aeropyles. The integumental petal is fused laterally with the stomal sense organ in the first instar. The interspiracular processes of the first instar are large, broad, and multibranched, like those of *T. wheeleri* Curran. The lateral spiracular complexes of the third instar are identical to those of *T. imperfecta* (Coquillett) and *T. wheeleri*, but different from nine other California congeners, which in turn differ from each other in type and number of sensilla comprising their metathoracic and abdominal, lateral spiracular complexes. The mouth hooks of the third instar of *T. vicina* are bidentate, not tridentate like 10 other *Trupanea* spp. examined from California. The life cycle of *T. vicina* in southern California is of the aggregative type. Most eggs are inserted between or through the tips of the phyllaries and parallel to and between the florets of closed, preblossom flower heads. The first instars feed within the floral tubes; whereas, the second instars feed mainly in ovules of preblossom flower heads or soft achenes of open heads. Most third instars feed in the centers of open or postblossom flower heads on the soft achenes. Pupariation occurs inside the mature flower heads, from which the adults later emerge. Limited reproduction occurs on wild hosts in southern California, but three to four, overlapping generations are produced on marigold from early summer (June) through November, or until frost. *Pteromalus* sp. (Hymenoptera: Pteromalidae) is reported as a probable solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Trupanea, Tagetes*, Asteraceae, marigold, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, host-plant range, parasitoid

This is the last paper in our recent series on *Trupanea*, one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California, though of little or no economic importance (Foote and Blanc 1963, Foote et al. 1993). *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until we published detailed life histories of 11 species from southern California (Cavender and Goeden 1982; Goeden 1987, 1988; Goeden et al. 1998a, b; Goeden and Teerink 1997b, 1998, 1999a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of

their immature stages (Cavender and Goeden 1982; Goeden et al. 1998a, b; Goeden and Teerink 1997b, 1998, 1999a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). In this paper we describe the life history and immature stages of a twelfth species, *T. vicina* (Wulp). Two additional species, *T. femoralis* (Thomson) and *T. radifera* (Coquillett) remain under study in southern California, but may not be completed and published before RDG retires.

Materials and Methods

This study was added to the series on *Trupanea* in 1997 following the discovery in October of an ornamental planting of marigold (*Tagetes* sp.) heavily infested with *T. vicina* just west of the University of California, Riverside, campus. Fortuitously, this discovery was followed by our chance sampling of infested mature flower heads of *Thymophylla* (= *Dyssodia*) *pentachaeta* var. *belenidium* (deCandolle) Strather in Shadow Valley (E Mojave Desert) ca. 13 km W of Mountain Pass at 1,110-m elevation, NE San Bernardino Co., on 6.xi.1997. This latter sample yielded additional specimens of immature stages and adequate data on phytophagy in a wild host plant, which had eluded us since 1991, when our field studies of *T. vicina* first began. Thus, the present study was based in large part on dissections of subsamples of flower heads collected from these two locations in the manner described by Goeden (1985, 1992). One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Seventeen eggs, 11 first-, eight second-, and 10 third-instar larvae, and five puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Three virgin males and two females obtained from emergence cages also were held in each of six, previously unused, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1998a, b), Goeden and Teerink (1997b, 1998, 1999a, b), Headrick and Goeden (1991), Knio et al. (1996a), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. vicina* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and currently maintained by RDG.

Results and Discussion

Taxonomy

Adult.—*Trupanea vicina* was first described by Wulp (1900) as *Urellia vicina*. It was transferred to *Trupanea* (as *Typanea*) by Hendel (1914). Foote (1965) designated a female from Orizaba, Mexico, now in the Natural History Museum as lectotype. Wulp (1900), Curran (1932), Malloch (1942), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern of the female and male, which unlike several North American *Trupanea* spp., is not sexually dimorphic (Foote et al. 1993).

Immature stages.—The egg, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Forty-one eggs of *T. vicina* dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.72 ± 0.006 (range, 0.64–0.80) mm long, 0.19 ± 0.001 (range, 0.17–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A)$_S$ peglike pedicel, 0.02 mm long, circumscribed by single row of oblong-elliptical aeropyles (Fig. 1B), with micopyle in center at apex surrounded by spokelike furrows, which may help channel sperm (Fig. 1C).

Eggs of all 12 species of *Trupanea* from California studied to date are similar in shape, color, and smoothness. Except for *T. bisetosa* (Coquillett) and *T. wheeleri* Curran with one or two rows of aeropyles (Knio et al. 1996a, Goeden and Teerink 1999b), the eggs of *T. vicina* and nine other species of *Trupanea* previously studied have only one row of aeropyles (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al. 1998a, b; Headrick and Goeden 1991; Teerink and Goeden 1998, 1999). The egg of *T. vicina* is longer on average than those of *T. actinobola* (Loew), *T. californica* Malloch, *T. imperfecta* (Coquillett), *T. pseudovicina* Hering, *T. signata* (Foote), and *T. wheeleri* (Goeden et al. 1998; Goeden and Teerink 1997b, 1998, 1999b; Headrick and Goeden 1991; Teerink and Goeden 1998); about as long as those of *T. bisetosa, T. jonesi* Curran, and *T. nigricornis* (Coquillett) (Goeden et al. 1998a, Knio et al. 1996a); and only shorter than the egg of *T. conjuncta* (Adams) (Teerink and Goeden 1998).

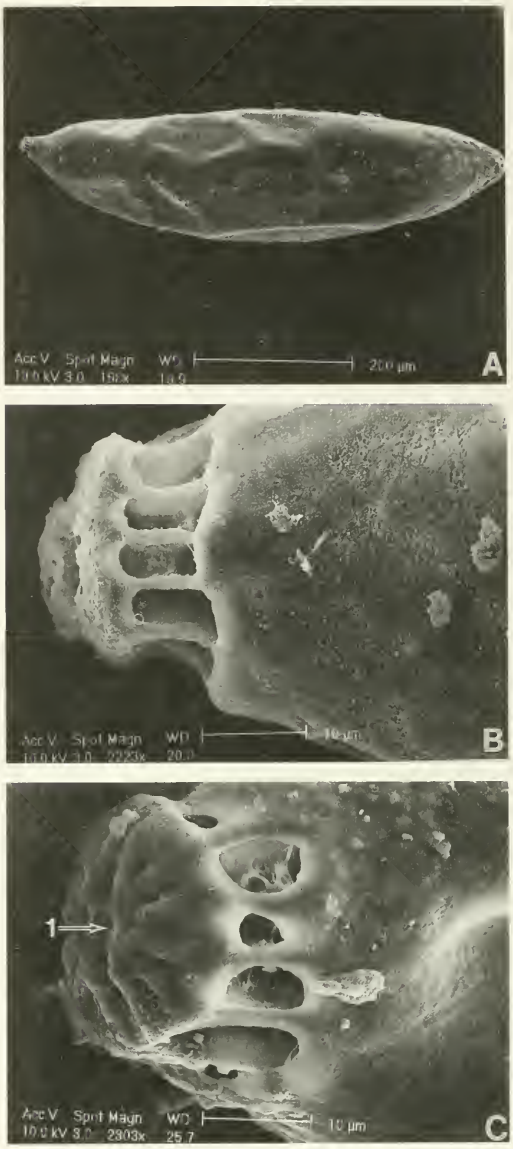

Fig. 1. Egg of *Trupanea vicina*: (A) habitus, anterior end to left; (B) pedicel, aeropyles; (C) pedicel apex, 1-micopyle.

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines; gnathocephalon smooth,

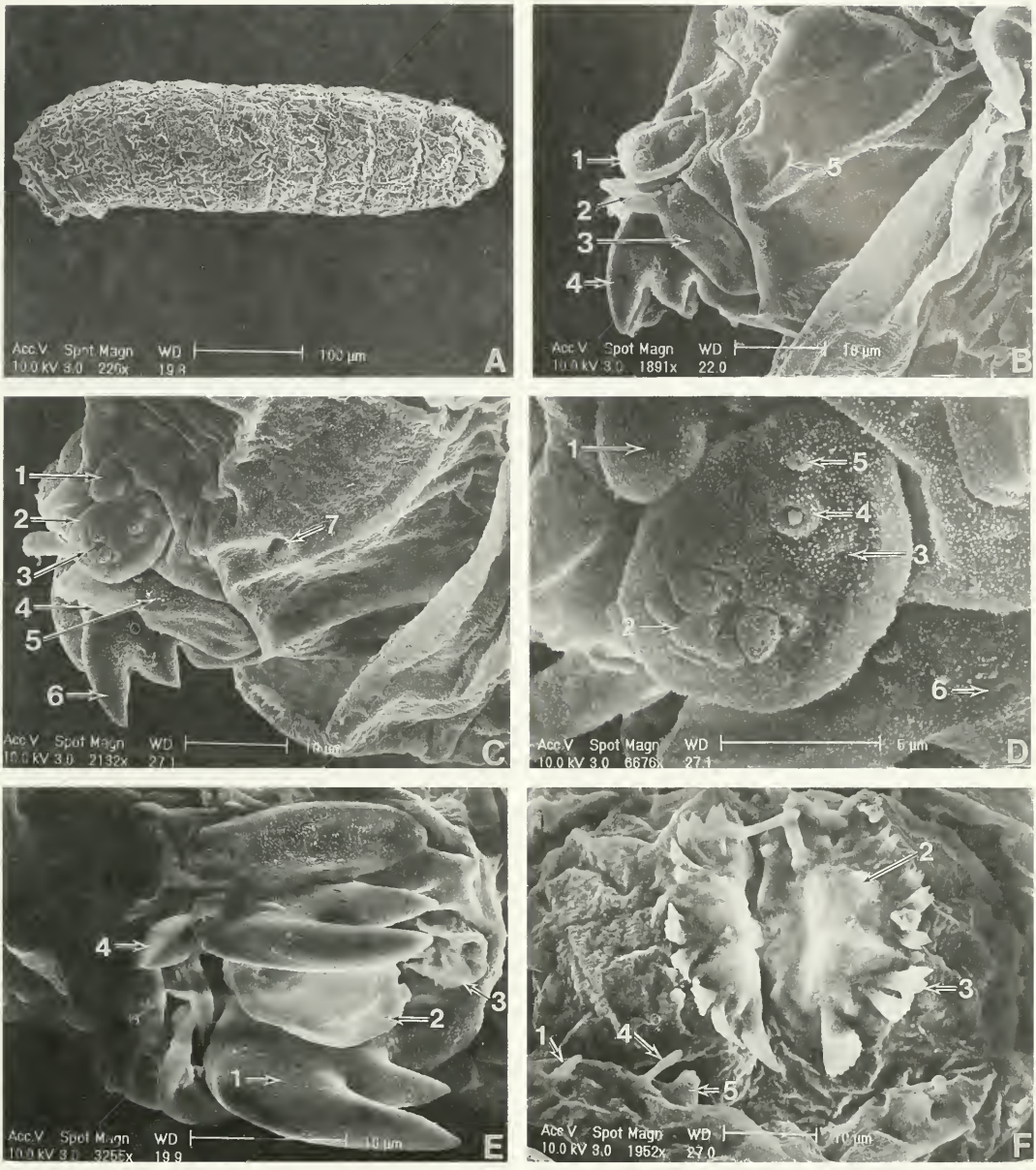

Fig. 2. First instar of *Trupanea vicina*: (A) habitus, anterior end to left; (B) gnathocephalon, lateral view, 1- anterior sensory lobe, 2- integumental petal, 3- stomal sense organ, 4- mouth hook, 5- pit sensillum; (C) gnathocephalon, dorsolateral view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- integumental petal, 5- stomal sense organ, 6- mouthhook, 7- pit sensillum; (D) anterior sensory lobe, 1- dorsal sensory organ, 2- terminal sensory organ, 3- pit sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- stomal sense organ; (E) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe, 3- labial lobe, 4- integumental petal; (F) caudal segment, 1- stelex sensillum, 2- rima, 3- interspiracular process, 4- intermediate sensory complex, medusoid sensillum, 5- intermediate sensory complex, stelex sensillum.

lacking rugose pads (Fig. 2B, C); dorsal sensory organ a dome-shaped papilla (Fig. 2C-1, D-1); anterior sensory lobe (Fig. 2B-1, C-2, D) bears the terminal sensory organ (Fig. 2C-3, D-2), pit sensory organ (Fig. 2D-3), lateral sensory organ (Fig. 2D-4) and supralateral sensory organ (Fig. 2D-5); stomal sense organ ventrad of anterior sensory lobe (Fig. 2B-3, C-5, D-6); mouth hooks bidentate (Fig. 2B-4, C-6, E-1); median oral lobe laterally flattened (Fig. 2E-2); labial lobe with two pore sensilla (Fig. 2E-3); pair of prominent integumental petals (Fig. 2B-2, C-4, E-4) dorsal to mouth hooks, each integumental petal is fused laterally with stomal sense organ (Fig. 2B-3, C-5); pit sensillum laterad of mouth lumen (Fig. 2B-5, C-7); anterior thoracic spiracle not present; caudal segment with two stelex sensilla dorsad and ventrad (Fig. 2F-1) of posterior spiracular plates; posterior spiracular plate bears two ovoid rimae, ca. 0.006 mm in length (Fig. 2F-2), and four interspiracular processes, each with 1–4, apically multidentated branches, longest measuring 0.008 mm (Fig. 2F-3); intermediate sensory complex consists of a stelex sensillum (Fig. 2F-4) and a medusoid sensillum (Fig. 2F-5).

The first instar is similar in general habitus and sensory structures to previously studied *Trupanea* species, except that the integumental petal is fused with the stomal sense organ (Goeden and Teerink 1997b, 1998, 1999a, b; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Like *T. wheeleri* (Goeden and Teerink 1999b), the interspiracular processes are large, broad, branched, and apically multidentate, and thus are far more elaborate than those of, for example, *T. arizonensis* (Goeden and Teerink 1999a), *T. conjuncta* (Teerink and Goeden 1998), and *T. jonesi* (Goeden et al. 1998a).

Second instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly (Fig. 3A), minute acanthae circumscribe intersegmental lines; gnathocephalon conical (Fig. 3B); dorsal sensory organ a dome-shaped papilla (Fig. 3C-1); anterior sensory lobe (Fig. 3C-2) bears the terminal sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5), pit sensory organ not shown; integumental petals separated from stomal sense organ (Fig. 3D); mouth hooks bidentate (Fig. 3B-1, C-6, D-1); median oral lobe laterally flattened, apically pointed, and with ventral lobe (Fig. 3C-7, D-2); labial lobe with two pore sensilla (Fig. 3D-3); minute acanthae circumscribe anterior margin of prothorax (Fig. 3B-2, C-8); rugose pads circumscribe prothorax posteriorad to acanthae (Fig. 3B-3, C-9); anterior thoracic spiracle bears three ovoid papillae (Fig. 3E); lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorsad and ventrad (Fig. 3F-1) of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.02 mm in length (Fig. 3F-2), and four interspiracular processes, each with 1–4 branches, longest measuring 0.016 mm (Fig. 3F-3); intermediate sensory complex consists of a medusoid sensillum (Fig. 3F-4) and a stelex sensillum (Fig. 3F-5).

The interspiracular processes of the second instar are similarly branched, though not as broad as the first instar, and apically pointed, not dentate. Unlike the second instars of *T. nigricornis, T. pseudovicina*, and *T. wheeleri*, the rugose pads laterad of the mouth lumen are not serrate (Goeden and Teerink 1998, 1999b; Knio et al. 1996a).

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. $4A)_S$ gnathocephalon conical (Fig. 4B), rugose pads laterad of mouth lumen with serrate margins (Fig. 4C-1); dorsal sensory organ a dome-shaped papilla (Fig. 4C-2); anterior sensory lobe (Fig. 4C) bears the terminal sensory organ (Fig. 4C-3), pit sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), and supralateral sensory organ (Fig. 4C-6); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 4C-7); mouth hooks biden-

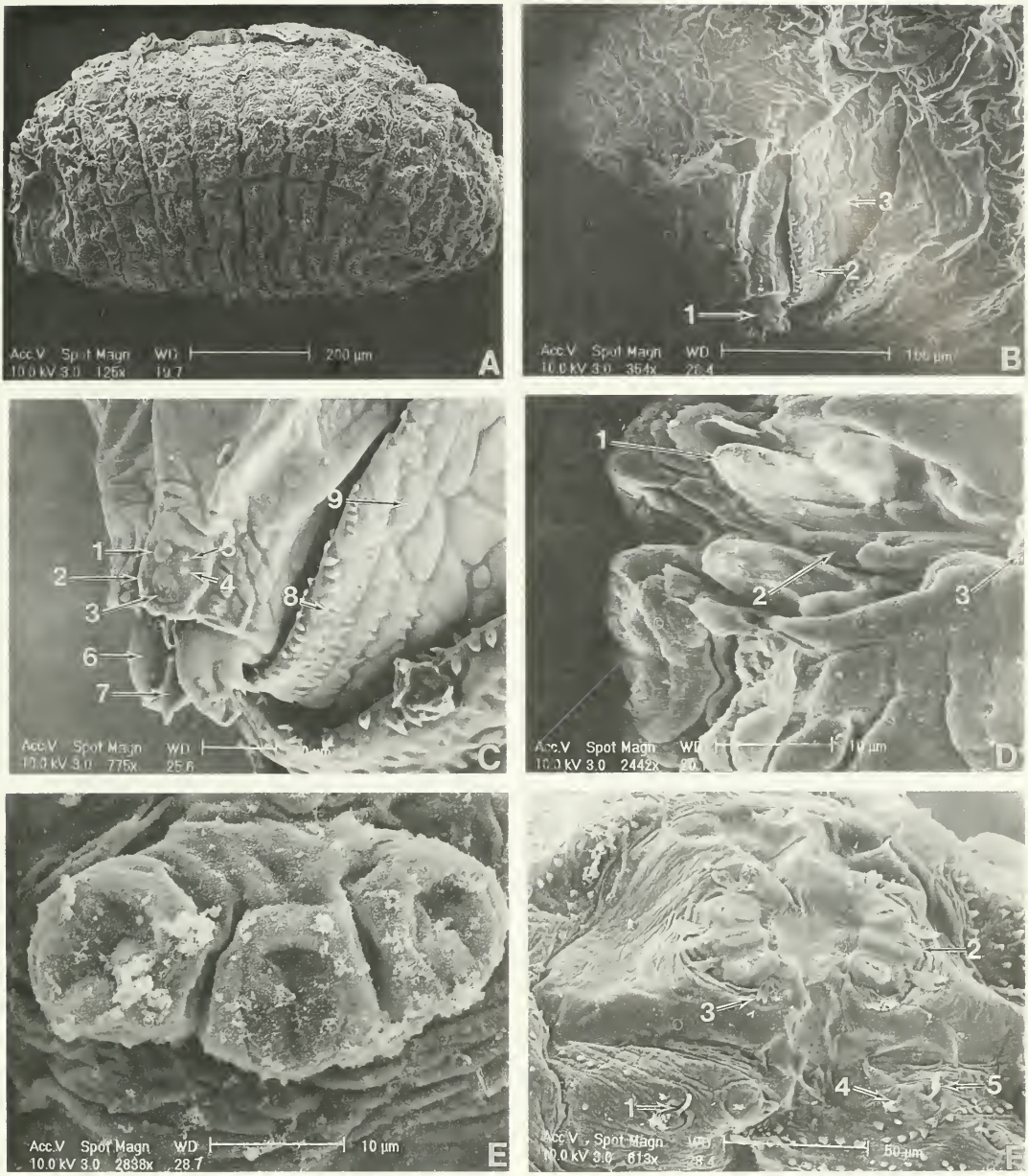

Fig. 3. Second instar of *Trupanea vicina*: (A) habitus, anterior end to left; (B) gnathocephalon and prothorax, lateral view, 1- mouth hook, 2- minute acanthae, 3- rugose pad; (C) gnathocephalon, dorsolateral view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- mouth hook, 7- median oral lobe, 8- minute acanthae, 9- rugose pad; (D) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe, 3- labial lobe; (E) anterior thoracic spiracle; (F) caudal segment, 1- stelex sensillum, 2- rima, 3- interspiracular process, 4- intermediate sensory complex, stelex sensillum, 5- intermediate sensory complex, medusoid sensillum.

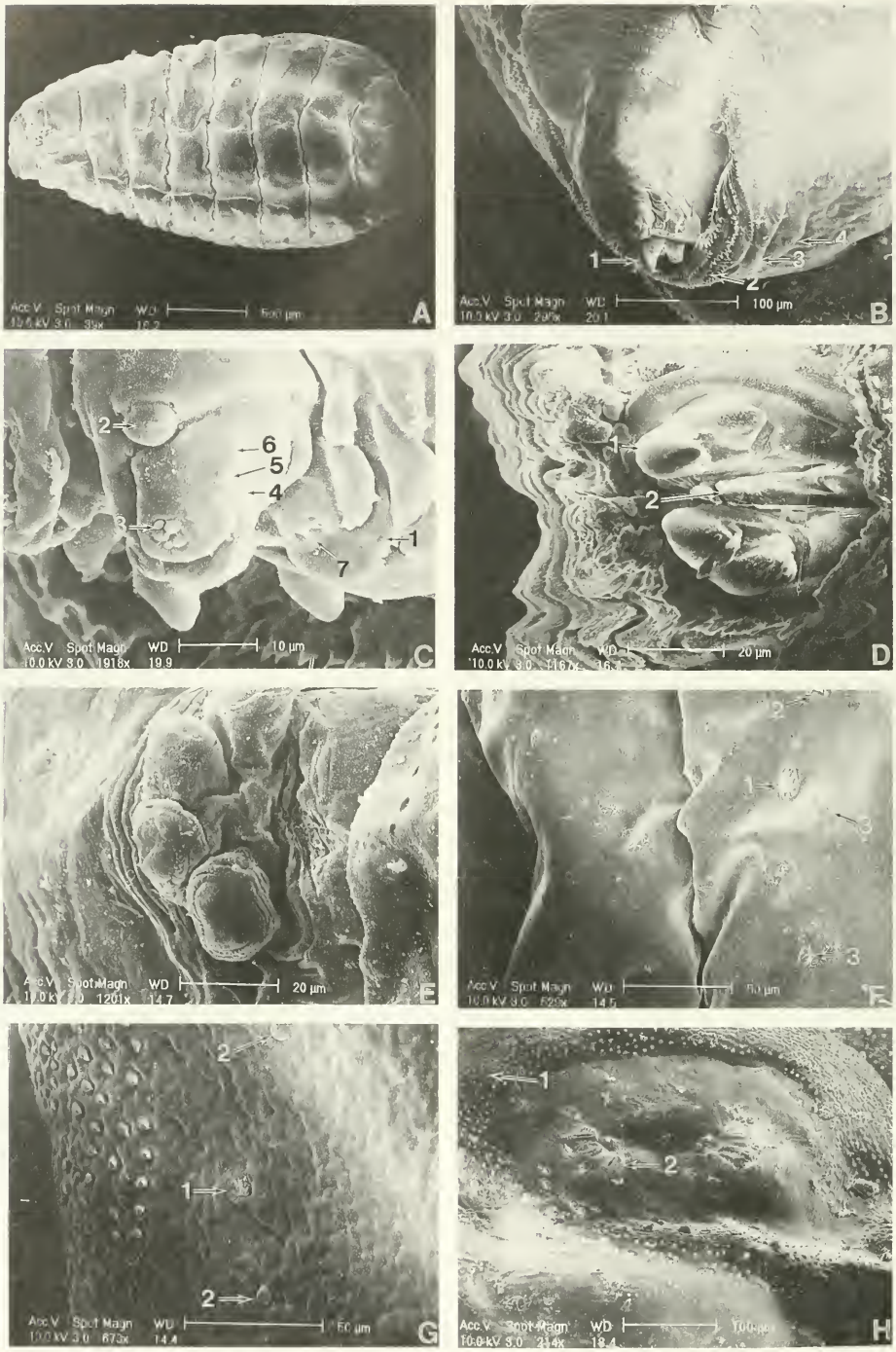

Fig. 4. Third instar of *Trupanea vicina*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, anteriolateral view, 1- mouth hook, 2- minute acanthae, 3- rugose pad, 4- verruciform sensillum; (C) anterior sensory lobe, 1- serrated rugose pad, 2- dorsal sensory organ, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ; (D) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe; (E) anterior thoracic spiracle; (F) meso- and metathorax (left to right), 1- spiracle, 2- stelex sensillum, 3- verruciform sensilla; (G) first abdominal segment, 1- spiracle, 2- verruciform sensilla; (H) caudal segment, 1- minute acanthae, 2- rima.

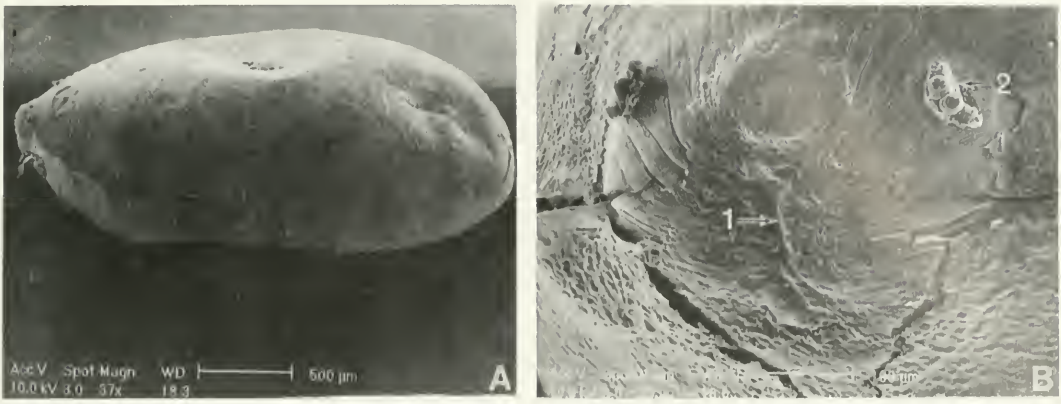

Fig. 5. Puparium of *Trupanea vicina*: (A) habitus, anterior end to left; (B) anterior end, 1- invagination scar, 2- anterior thoracic spiracle.

tate (Fig. 4B-1, 4D-1); median oral lobe laterally flattened (Fig. 4D-2); prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-2); rugose pads circumscribe prothorax posteriorad to acanthae (Fig. 4B-3); two rows of verruciform sensilla circumscribe prothorax posteriorad to rugose pads (Fig. 4B-4); anterior thoracic spiracle on posterior margin of prothorax bears 3–4 rounded papillae (Fig. 4E); mesothorax and metathorax not circumscribed anteriorly with verruciform sensilla (Fig. 4F); mesothoracic and metathoracic lateral spiracular complexes each consist of a spiracle (Fig. 4F-1), a stelex sensillum (Fig. 4F-2), and two verruciform sensilla (Fig. 4F-3); abdominal lateral spiracular complex consists of a spiracle (Fig. 4G-1) and two verruciform sensilla (Fig. 4G-2); caudal segment circumscribed by minute acanthae (Fig. 4H-1); two stelex sensilla, dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.03 mm in length (Fig. 4H-2), and four interspiracular processes, each with 2–3 branches, longest measuring 0.02 mm (seen but not shown); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum (seen but not shown).

The third instar bears serrated rugose pads similar to the third instars of *T. imperfecta, T. jonesi, T. nigricornis, T. pseudovicina, T. signata*, and *T. wheeleri* (Goeden and Teerink 1997b; 1998, 1999b; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1999). Unlike the third instars of 11 other *Trupanea* spp. examined that have tridentate mouth hooks (Goeden and Teerink 1997b, 1998, 1999a, b; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999), the mouth hooks of the third instar of *T. vicina* are bidentate (Fig. 4D-1). Compared to three papillae in the second instar, the anterior thoracic spiracle of third instar bears 3–4 papillae (sometimes different on the same individual, Fig. 5B). Neither the meso- or metathorax are so circumscribed by verruciform sensilla; whereas, only the mesothorax is circumscribed in *T. nigricornis* (Knio et al. 1996a). Both the meso- and metathorax are circumscribed by verruciform sensilla in *T. arizonensis* and *T. imperfecta* (Goeden and Teerink 1999a, Teerink and Goeden 1999). The third-instar, metathoracic and abdominal spiracular complexes are identical to those of *T. imperfecta* (Teerink and Goeden 1999) and *T. wheeleri* (Goeden and Teerink 1999b). This is the first reported instance in which not only two, but three species of *Trupanea* share the same type and number of sensilla in the metathoracic and abdominal lateral spiracular complexes; the complexes of all nine other California *Trupanea* species studied have differed (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al.

1998, 1999; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Other pairs of congeneric species in other genera are known to share the same number and type of sensilla in the lateral spiracular complexes, e.g., *Procecidochares kristineae* and *P. lisae; Aciurina idahoensis* and *A. michaeli; A. thoracica* and *A. trixa* (Goeden and Teerink 1996a, b. 1997a; Headrick and Goeden 1993; Headrick et al. 1997).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae, two stelex sensilla, dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, and four interspiracular processes, each with 2–3 branches; intermediate sensory complex (seen but not shown) consists of a medusoid sensillum and a stelex sensillum. Thirty-seven puparia averaged 2.87 ± 0.05 (range, 2.28–3.56) mm in length; 1.32 ± 0.02 (range, 1.00–1.56) mm in width.

Distribution and Hosts

The distribution of *T. vicina* as mapped by Foote et al. (1993) included multiple locations in all States bordering Mexico, i.e., Arizona, California, New Mexico, and Texas, plus two locations in Nevada, and a single location in Georgia. The last record could represent a radical eastward extension of its range, perhaps resulting from its introduction along with marigold, one of more than 30 species of cultivated, aromatic, flowering herbs in the genus *Tagetes* originating in Mexico and widely cultivated in the Southwest (Bailey 1975). More likely, however, Gary Steck (in litt. 1998) suggests that the Georgia record for a single specimen collected in 1896 probably represents an error, as this would then be the sole record for this fly in the Southeastern U.S. during the past century.

Foote (1960) first reported *T. vicina* as reared from marigold, which belongs to the subtribe Pectidinae in the tribe Helenieae of the Asteraceae (Hickman 1993, Bremer 1994). However, unlike *T. pseudovicina*, which is monophagous on *Porophyllum gracile* Bentham from this same tribe and subtribe in southern California (Goeden and Teerink 1998), *T. vicina* does not attack *P. gracile*, but has been reported by Goeden (1985, 1992) from four other genera and species of uncultivated ("wild"), native host plants belonging to the Pectidinae and Helenieae in southern California, i.e., *Adenophyllum* (= *Dyssodia*) *porophylloides* (A. Gray) Strother, *Thymophylla pentachaeta* var. *belenidium, Nicolletia occidentalis* A. Gray, and *Pectis papposa* Harvey and A. Gray var. *papposa*, as listed by Hickman (1993).

A quandary is presented by the host record dating from 1982 for three females of *T. vicina* from *Coreopsis douglasii* (de-Candolle) H.M. Hall in Goeden (1985), a genus from which this tephritid since has never again been reared, even during intensive and extensive field study of two principal tephritid associates of *Coreopsis* spp., *Dioxyna picciola* (Bigot) (Headrick et al. 1996) and *T. jonesi* (Goeden et al. 1998a). This host record for *T. vicina* is suspect, or at least atypical, because *Coreopsis* belongs to an entirely different tribe of Asteraceae, the Heliantheae, subtribe Coreopsidinae (Bremer 1994). The identity of these three specimens, still in the research collection of RDG, has been reconfirmed. Possible explanations include contamination of the sample with flower heads accidentally collected from an intergrown or nearby host plant, or oviposition mistakes by a female *T. vicina*, suspected to have occurred with at least one other, congeneric, sympatric, stenophagous (narrow host range), desert tephritid, *T. pseudovicina* (Goeden and Teerink 1998). Also like several other tephritid species that we have studied, i.e., *Trupanea conjuncta* (Goeden 1987), *T. pseudovicina* (Goeden and Teerink), *Tomoplagia cressoni* Aczél (Goeden and

Headrick 1991), and *Zonosemata vittigera* (Coquillett) (Goeden and Ricker 1971), *Trupanea vicina* represents a native southern California tephritid closely associated with native host-plants primarily distributed in Mexico and southward, where they remain little studied.

Biology

Egg.—In 31 closed, preblossom, immature flower heads of *Tagetes* sp., 27 (66%) of 41 eggs were inserted between or through the tips of the phyllaries and parallel to and between the florets; the remainder were oviposited through the phyllaries laterally and deposited loosely atop the florets and parallel to the receptacle in the conical space beneath the appressed apices of the phyllaries (Fig. 6A). All eggs were oviposited pedicel-last. Only three (10%) of 31 flower heads with eggs respectively contained 5, 1, and 2 florets damaged by ovipositional probing; no eggs were inserted into plant tissues. The diameters of the receptacles of 31 flower heads containing eggs averaged 2.9 ± 0.1 (range, 1.9–3.7) mm, and these heads contained an average of 1.5 ± 0.1 (range, 1–3) eggs, all oviposited singly. If more than one egg was found in a head, they were always separated, and thus, probably oviposited by different females.

Larva.—Upon eclosion, first instars tunneled into the apical end of an unelongated floral tube of an immature floret (Fig. 6B). An average of 1.3 ± 0.2 (range, 1–2) first instars was found feeding within eight, closed, preblossom, marigold flower heads, the receptacles of which averaged 3.2 ± 0.1 (range, 2.8–4.0) mm in diameter. These infested heads contained an average of 61 ± 3 (range, 48–78) florets, of which an average of only 1.9 ± 0.5 (range, 1–5) floral tubes, or 3.2% (range, 1.3–8.9%), were damaged. First instars continued to feed down the floral tubes towards the ovules. No ovules or receptacles within these eight infested flower heads were abraded or pitted by first-instar feeding.

Second instars fed mainly in ovules of preblossom marigold flower heads or in soft achenes of open heads (Fig. 6C). Most second instars fed separately with their mouthparts directed towards the receptacles within adjacent ovules/soft achenes, but well above the receptacles (Fig. 6C). Receptacles of 21 flower heads containing second instars were undamaged and averaged 3.9 ± 0.1 (range, 2.9–4.7) mm in diameter. These flower heads contained an average of 1.6 ± 0.3 (range, 1–6) second instars that had destroyed an average of 7.1 ± 1.1 (range, 2–26) ovules/soft achenes, or 11.7% (range, 3.1–34%) of an average total of 61 ± 3 (range, 38–83) ovules/soft achenes per head.

Most third instars confined their feeding to soft achenes in the centers of open or postblossom flower heads of marigold (Fig. 6D) and *Thymophylla pentachaeta* (Fig. 6E). In 18 marigold flower heads (Fig. 6D) averaging 3.6 ± 0.1 (range, 2.3–4.6) mm in diameter and containing an average of 1.4 ± 0.2 (range, 1–4) third instars, an average of 11.4 ± 1.0 (range 1–26) soft achenes were damaged, or 23% (range, 5–67%) of an average total of 56 ± 4.2 (range 21–110) soft achenes per head. In 42 smaller flower heads of *T. pentachaeta* (Fig. 6E) averaging 1.4 ± 0.02 (range, 1.1–1.7) mm in diameter and each containing an average total of 72 ± 2.1 (range 46–105) soft achenes and one third instar, an average of 26.5 ± 0.9 (range 16–38) soft achenes were damaged, or 37.5% (range, 25–52%). Third instars in flower heads of both hosts fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 6E). Only 2 (4.7%) of 42 receptacles in *T. pentachaeta* were pitted by third instar feeding; none in 18 infested marigold flower heads. Upon completing their feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 6F).

Pupa.—Flower heads containing puparia (Fig. 6F) reflected the greatest damage produced by the seed-feeding larvae of *T. vi-*

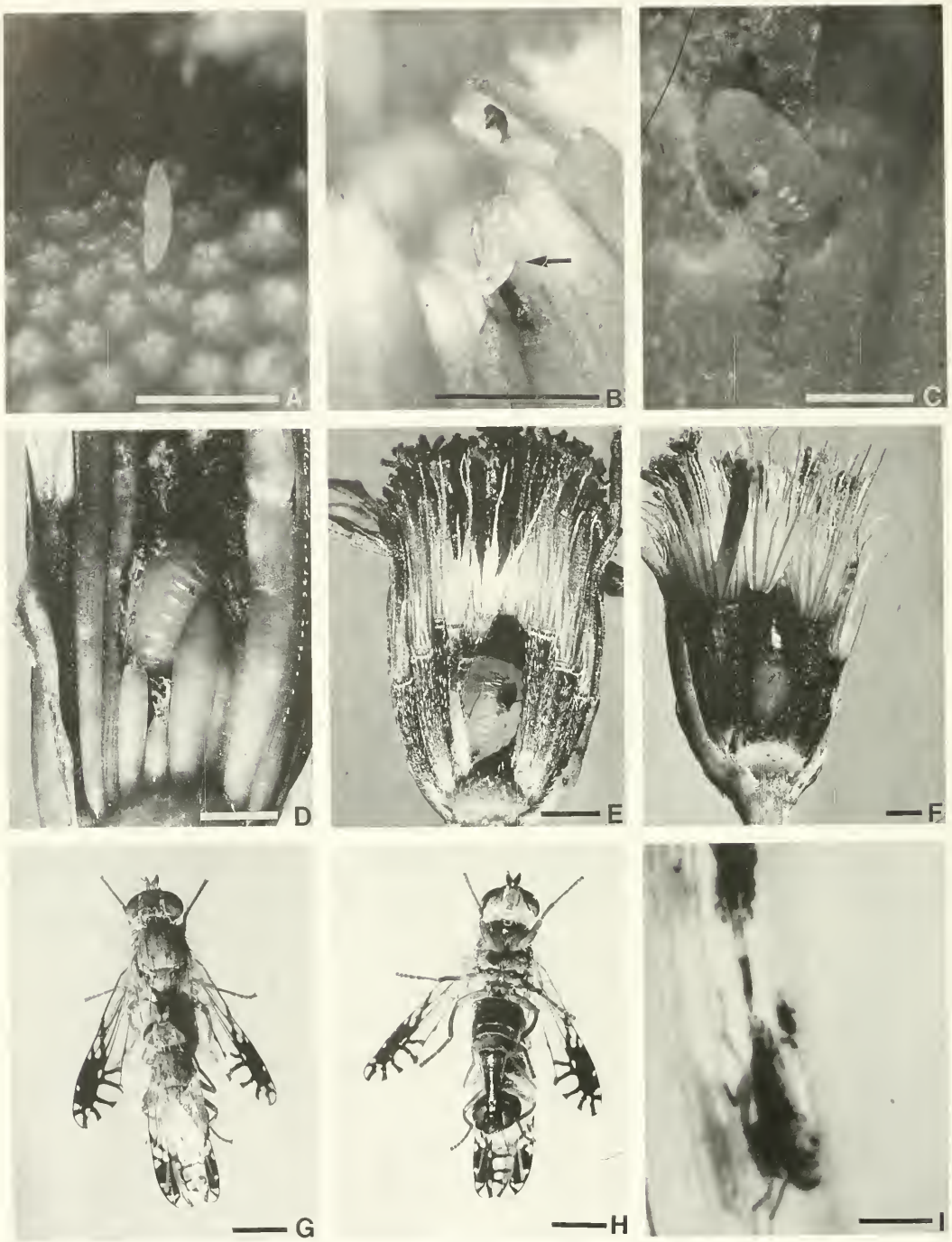

Fig. 6. Life stages of *Trupanea vicina*: (A) egg laid atop florets in immature flower head of marigold, (B) early first instar (arrow) feeding at apex of floret in marigold, (C) second instar feeding in floral tube and ovule in flower head of marigold, (D) third instar feeding on ovules in flower head of marigold, (E) third instar feeding among soft achenes in center of open flower head of *Thymophylla pentachaeta*; (F) puparium in flower head of *T. pentachaeta*, (G) mating pair, dorsal view; (H) mating pair, ventral view; (I) male withdrawing aculeus at termination of mating (blurred because entire process took only 3–4 sec, see text). Lines = 1 mm.

cina within flower heads sampled. The receptacles of 34 infested marigold flower heads containing puparia averaged 3.6 ± 0.2 (range, 2.3–8.2) mm in diameter and bore an average total of 53.9 ± 1.6 (36–73) soft achenes/florets, of which an average of 15.3 ± 1.2 (range, 4–35) soft achenes/florets or 29% (range, 7–78%) were damaged. The receptacles of 12 (35%) of the 34 flower heads were pitted. These 34 heads contained an average of 1.5 ± 0.2 (range, 1–4) puparia. All puparia of *T. vicina* were found in the center of the flower heads with their anterior ends facing away from the receptacles and their long axes perpendicular to the receptacles (Fig. 6F).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as unmated males averaged 94 ± 8 (range, 14–147) days, and virgin females averaged 72 ± 6 (range, 29–130) days. Such longevities are commensurate with the aggregative type of life cycle ascribed below to this tephritid.

The premating and mating behaviors of *T. vicina* were not studied in the field, but we did study these behaviors using petri dish arenas found to be so useful with many other noncongeneric, nonfrugivorous, tephritid species (Headrick and Goeden 1994). Unlike most other *Trupanea* spp. that we have studied, at least two matings of *T. vicina* were observed in these arenas, but only when more than single pairs of flies were caged together. This crowding factor should be addressed experimentally with other *Trupanea* spp. Before we began our use of petri dish arenas, mating under crowded conditions also was observed in mass sleeve-cagings of *T. bisetosa* adults (Cavender and Goeden 1982). Premating behaviors observed with *T. vicina* were abdominal pleural distensions by males (Headrick and Goeden 1994, Knio et al. 1996b, Goeden et al. 1998a) and wing hamations combined with supinations as reported for *T. jonesi* (Goeden et al. 1998a), but without rapid wing vibrations, by both sexes. Two matings (Fig. 6G, H) were observed during the early afternoon with different pairs of flies of 25- and 28-min duration; similarly short mating duration have been reported for all congeners studied to date (Cavender and Goeden 1982, Goeden et al. 1998a, Headrick and Goeden 1994, Knio et al. 1996b). Each pair apparently mated only once, as reported with *T. jonesi* (Goeden et al. 1998a). The copulatory position of each pair of *T. vicina* was as described for *T. jonesi* (Goeden et al. 1998a). Disengagement, rarely observed in *Trupanea* spp. (Headrick and Goeden 1994, Knio et al. 1996b, Goeden et al. 1998a), was seen once and involved a male turning 180° as he rapidly dismounted and walked away from the female while pulling free his genitalia, all in 3–4 sec. (Fig. 6I). As with other *Trupanea* spp., no post-copulatory behavior was observed other than individual groomings by both flies, and as the male recoiled his genitalia.

Seasonal history.—The life cycle of *T. vicina* in southern California follows an aggregative pattern in which the long-lived adults overwinter while in reproductive diapause and then aggregate to mate on preblossom host plants in the spring (March–April) (Headrick and Goeden 1994). They reproduce limitedly at first on wild hosts, e.g., *Adenophyllum porophylloides*, in the low-elevation Colorado Desert, then in the higher-elevation, Mojave Desert, and on occasional host plants scattered in chaparral of the interior valleys (Munz 1974, Hickman 1993). However, the major host plants on which *T. vicina* reproduces in southern California are various varieties of herbaceous, cultivated marigold, widely planted as summer annuals. This tephritid conceivably produces three to four overlapping, nondiscrete generations on marigold from early summer (June) until as late as November, or until frost occurs. Fortunately, for both gardeners and *T. vicina*, there is no loss of ornamental quality to infested marigold flower heads, and thus no need for chemical control, because most feeding and pupariation occur in the mature heads nor-

mally pruned or left to dry and abscise. Thus, like *T. signata* (Goeden and Teerink 1997b), this native tephritid species has adapted to and benefited from human floricultural practices.

Natural enemies.—*Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from mature flower heads of *Adenophyllum porophylloides* bearing third instars and puparia as a probable solitary, larval-pupal endoparasitoid of *T. vicina*.

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RANGE EXTENSION OF *PALAEMNEMA DOMINA* CALVERT (ODONATA: PLATYSTICTIDAE) TO SOUTHEASTERN ARIZONA, U.S.A.: A NEW ODONATE FAMILY FOR THE UNITED STATES

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Abstract.—The occurrence of a population of *Palaemnema domina* Calvert in southeastern Arizona, U.S.A. extends the known northern range limit of this species from Chihuahua, Mexico. It is the first record of the Platystictidae for the United States. Notes on adult perching habits and a brief habitat description are provided.

Key Words: damselflies, Platystictidae, Zygoptera, Odonata, Arizona

Four families of damselflies (suborder Zygoptera) have traditionally been recorded and diagnosed for the United States: Calopterygidae, Lestidae, Protoneuridae, and Coenagrionidae (Westfall 1987, Borror et al. 1989, Westfall and Tennessen 1996). We report the addition of a fifth family, Platystictidae, to the United States Zygoptera fauna. The Platystictidae are a pantropical family containing a single Neotropical genus, *Palaemnema* Selys, of 42 described species. Westfall and May (1996) provide an excellent introduction to the taxon.

A single male *Palaemnema domina* Calvert was collected by JH on the Muleshoe Ranch Preserve along Hot Springs Creek about 2 miles north of Hookers Hot Springs, Arizona, on 20 August 1996. Subsequent collections and observations by JH and JH and RWG were conducted on 20–21 September 1996; and on 17 July and 10 August 1997. These collections extend the known range of *P. domina* approximately 500 km from its previous northernmost collection locality in Chihuahua, Mexico, near Yepachic (S. Dunkle, personal communication). The species has also been recorded from Morelos and Nayarit states, Mexico (Paulson and Gonzalez-Soriano 1996), from desert streams in Chiapas and Oaxaca states, Mexico, as well as eastern Guatemala and Nicaragua (T. W. Donnelly, personal communication) and Honduras (Paulson 1997).

Palaemnema domina Calvert
(Fig. 1)

Palaemnema domina Calvert 1905: 134, 137 (description, key); Calvert 1905: 145–212. Odonata.

New records.—U.S.A., Arizona, Cochise County, Hot Springs Creek, 1190 m: VIII-20-96, J. D. Hoekstra, 1 ♂ (TWD); VII-17-97, J.D. Hoekstra, 1 ♀ (UAIC); Hot Springs Creek, 1,175 m, 32°21.31N, 110°15.63W: IX-20-96, J.D. Hoekstra and R. W. Garrison, 6 ♂, 2 ♀ (RWG), 1 ♀ (TWD); IX-21-96, J. D. Hoekstra and R. W. Garrison, 1 ♂ (RWG); VIII-10-97, J. D. Hoekstra, R. W. Garrison, J. Garrison, P. Garrison, 1 ♂, 1 ♀

Fig. 1. *Palaemnema domina*, adult male perching near base of tree. Photo by Rosser Garrison.

(UAIC), 12 ♂, 1 ♀ (RWG), S. Dunkle, 10 ♂, 2 ♀ (SD).

Abbreviations: RWG = R. W. Garrison personal collection. UAIC = University of Arizona Department of Entomology Insect Collection. TWD = T. W. Donnelly personal collection. SD = S. W. Dunkle personal collection.

Adult behavior.—Adults of *Palaemnema domina* aggregate in shady microhabitats and avoid the sunny situations usually favored by Odonata. When the species was first discovered at Hot Springs Creek, males were active during a light mid-afternoon rain when all other odonates had ceased activity. On hot, clear days (air temperature 30°C or higher), adults have been found only in humid, dark, cave-like riparian roosting sites. These cavities are formed within piles of woody debris that are heaped over the tangled root matrices at the bases of large riparian trees. Such flood-created habitats are often found several meters from the stream, and must be subject to violent disturbance and alteration during flash floods.

Several adults of both sexes aggregate within roosting sites; up to eight males have been counted from a single site (S. W. Dunkle, personal communication). Such troglodytic perching behavior is unusual for odonates, but is typical of Platystictidae, which commonly aggregate in shady roosting areas (T. W. Donnelly, personal communication). Similar reclusive behavior was observed for *Palaemnema desiderata* Selys, an Atlantic coast Mexican species found along humid, largely shaded lowland streams. In this case, several individuals of both sexes were observed roosting within densely vegetated microhabitats (Garrison and Gonzalez 1988). The reproductive behavior of *P. domina* is unknown. In a Mexican population of *Palaemnema desiderata*, copulation and oviposition are initiated just before sunrise. Eggs are deposited in the woody stems of riparian vegetation overhanging the stream (Gonzalez et al. 1982).

We observed males of *P. domina* perching in full sun at 10:30 am on young cottonwoods at streamside when humidity remained high (air temp. 21°C). By 11:30 on the same day, all adults had moved to heavily shaded perching sites.

Habitat description.—Hot Springs Creek is a small perennial stream south of the Galiuro Mountains in southeastern Arizona. The stream and its watershed are contained within the Muleshoe Ranch Cooperative Management Area, a 49,120-acre area managed for biodiversity protection by the Nature Conservancy, U.S. Forest Service, and U.S. Bureau of Land Management. *Platanus wrightii* Watson (Arizona sycamore), *Populus fremontii* Watson (Fremont cottonwood), and *Salix spp.* (willows) are the dominant riparian trees. The stream at summer base flow is 1.5–2 m wide in the area visited by the authors. Midstream depth is 30–50 cm.

The stream hosts several species of native fish and amphibians and a diverse community of aquatic insects. Several of the species present have Mexican biogeographic affinities; a waterscorpion, *Curicta pronotata* Kuitert (Hemiptera: Nepidae), at the northern limit of its range has been collected from a tributary to the habitat (Hoekstra and Smith 1998). The thermal regime of Hot Springs Creek is poorly understood, but could be significantly affected by geothermal inputs. Hot springs (outflow 52°C) and warm springs (outflow 33°C) are found upstream of the study area but do not drain directly into the perennial part of the stream (U.S. Geological Survey staff, personal communication).

Family Level Taxonomy of United States Zygoptera

With the discovery reported here, keys to the U.S. families of Zygoptera should be revised to include Platystictidae. For adults, this can be accomplished with addition of a couplet to separate platystictids from Protoneuridae. The diagnostic character is the unique short crossvein linking Cu with the wing margin proximal to Ac in Platystictidae (Westfall and May 1996). For larvae, most keys to the North American Zygopteran families segregate Calopterygidae and Lestidae first, based on antennal and premental characters. Once these families have been separated, the diagnostic character for Platystictidae is the medial cleft of the prementum indicated by a deep sulcus (Westfall and May 1996). Several other peculiarities distinguish the unusual larvae, which have been described as "termite-like" in general appearance (Westfall 1987).

Barring exotic species introductions, we expect that additional discoveries of new Zygopteran families are unlikely in the contiguous U.S. One exception might be southern Texas where collectors may discover Pseudostigmatidae. Two genera (*Mecistogaster* Rambur and *Pseudostigma* Selys) are known from Tamaulipas and Neuvo Leon states in neighboring Mexico (Westfall and May 1996). However, their large size and conspicuous behavior make it unlikely that these damselflies would have been overlooked in this heavily populated region.

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REVIEW OF THE NEW WORLD TREEHOPPER TRIBE STEGASPIDINI (HEMIPTERA: MEMBRACIDAE: STEGASPIDINAE): II: *LYCODERES* GERMAR, *OEDA* AMYOT AND SERVILLE, AND *STEGASPIS* GERMAR

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Abstract.—Three genera in the treehopper tribe Stegaspidini Haupt—*Lycoderes* Germar, *Oeda* Amyot and Serville, and *Stegaspis* Germar—are redescribed and illustrated based on adult and nymphal morphology. *Lycoderes* has 36 valid species, including ***L. nathanieli* Cryan, new species**; *Oeda* has 4 valid species and *Stegaspis* has 2. Six previously described *Lycoderes* species are here placed to subgenus for the first time: *L. fernandezi* Strümpel, *L. luteus* Funkhouser, *L. phasianus* Fowler, and *L. serraticornis* Fowler are included in the subgenus *Lycoderides* Sakakibara; *L. capitatus* Buckton and *L. minamen* (Buckton) are included in the subgenus *Lycoderes* Germar. An updated taxonomic key and a complete species checklist, including all synonymies, are given for each genus.

Key Words: Membracidae, Stegaspidini, *Lycoderes, Oeda, Stegaspis,* taxonomy

This work, the second in a series of three publications on the treehopper tribe Stegaspidini (Hemiptera: Membracidae: Stegaspidinae), includes redescriptions of the genera *Lycoderes* Germar, *Oeda* Amyot and Serville, and *Stegaspis* Germar. The genera *Bocydium* Latreille, *Lirania* Stål, and *Smerdalea* Fowler were treated in part I (Cryan and Deitz 1999a); *Flexocentrus* Goding, *Stylocentrus* Stål, and *Umbelligerus* Deitz will be addressed in part III (Cryan and Deitz, in press). Part I also included an introduction to this review series, explanations and illustrations of relevant morphological features, a redefinition of the tribe Stegaspidini, and a taxonomic key for the identification of included genera.

MATERIALS AND METHODS

Methods used in this work were described in part I (Cryan and Deitz 1999a). The following codens are used herein to refer to the collections in which relevant specimens are located or have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†) following the coden.

AMNH: American Museum of Natural History, New York, New York, USA.

BMNH: Department of Entomology, The Natural History Museum, London, United Kingdom.

BPBM: Department of Entomology, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

CNCI: Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Re-

search Branch, Ottawa, Ontario, Canada.

EMUS: Entomological Museum, Department of Biology, Utah State University, Logan, Utah, USA.

INBC: Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica.

IZAV: Instituto de Zoologiá Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.

MZLU: Museum of Zoology, Lund University, Helgonavägen, Lund, Sweden.

NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.

QCAZ: Quito Catholic Zoology Museum, Departamento de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

SEMC: Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

SHMC†: S. H. McKamey Collection, currently at the United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, % National Museum of Natural History, MRC-168, Washington, D.C., USA.

TKWC†: T. K. Wood Collection, currently at the Department of Entomology and Applied Ecology, University of Delaware, Newark, Delaware, USA.

UCDC: The Bohart Museum of Entomology, University of California, Davis, California, USA.

USNM: Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

ZMUH: Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg, Germany.

Following each distribution record in the text is either a coden (see above) or a superscript number. Codens refer to a collection that includes specimens validating that record (only one collection is listed in most cases, although multiple collections may have specimens validating the distribution record); superscript numbers document records from the literature that have not been confirmed in this work—references are: [1]Metcalf and Wade 1965a, [2]Ceballos-Bendezú 1980a, and [3]Remes-Lenicov 1976b. Unverified distribution records from the literature should be used with caution, as some may be based on misidentified specimens.

The location and structure of suprahumeral horns vary greatly within the tribe Stegaspidini, and even within some genera; nevertheless, the nature of these pronotal extensions usually provides excellent taxonomic features at the specific and generic levels. We consider any pronotal extensions located above the humeral angles to be suprahumeral horns. Thus, the unbranched processes of *Lycoderes* and *Oeda* spp. (Figs. 2–3, 11, 17–18), the stalked bulbs of *Bocydium* spp. (Cryan and Deitz 1999a: figs. 9, 11, 13), and the sometimes trifurcating horns of *Smerdalea* spp. (Cryan and Deitz 1995a: figs. 2, 9, 16) are homologous.

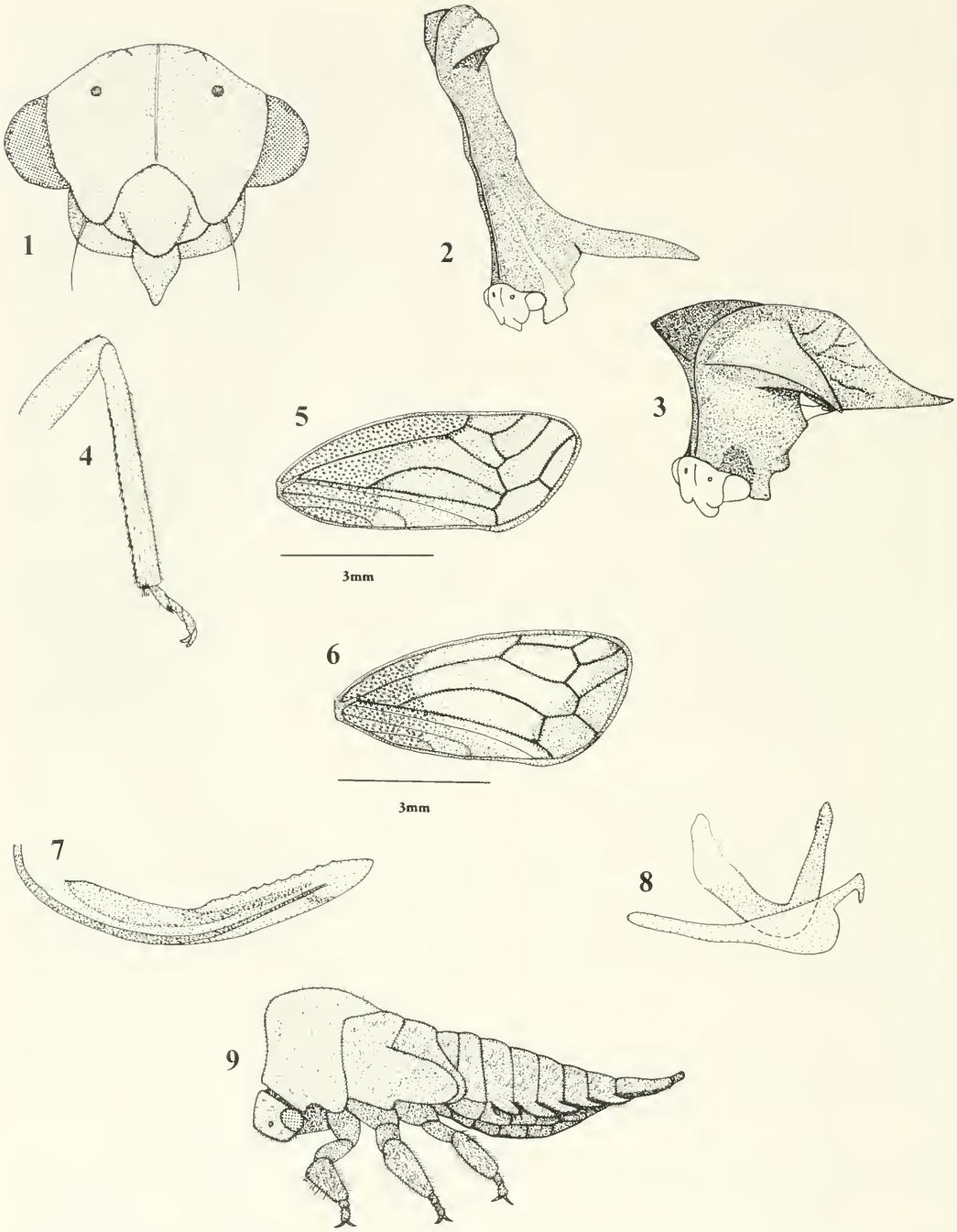
Genus *Lycoderes* Germar, 1835a

Lycoderes Germar 1835a: 259. Type species: *Centrotus ancora* Germar 1821a, by original designation.

Sycoderes [sic] Spinola 1850a: 54.

Diagnosis.—Pronotum elevated, often foliaceous, bearing apical or subapical suprahumeral horns; foliate lobes of the head not covering the postclypeus.

Adult.—*Dimensions* (mm): Total length 5.0–8.7. *Structure: Head* (Figs. 1–3): Finely setose; dorsal projections either very small or absent; ocelli on or above centro-ocular line; foliate lobes rounded; postcly-



Figs. 1–9. *Lycoderes* species. 1, *L. amazonicus,* head, anterior aspect (face). 2, *L. amazonicus,* head, pronotum, and scutellum, anterolateral aspect. 3, *L. mitratus,* head, pronotum, and scutellum, anterolateral aspect. 4, *L. mitratus,* left metathoracic femur, tibia, and tarsus, ablateral aspect. 5, *L.* (*Lycoderides*) *amazonicus,* right forewing. 6, *L.* (*Lycoderes*) *ancora,* right forewing. 7, *L. mitratus,* female second valvulae, lateral aspect. 8, *L. mitratus,* male aedeagus and left style, lateral aspect. 9, *L. marginalis,* late-instar nymph, lateral aspect.

peus usually strongly trilobed. *Thorax:* Pronotum (Figs. 2–3): Metopidium elevated into compressed anterior horn of variable length, with suprahumeral horns at (or just below) apex; suprahumeral horns always unbranched, of variable size and shape; posterior process variable (foliaceous, semi-foliaceous, or simple), completely concealing scutellum in some species (Fig. 2), not concealing scutellum in others (Fig. 3). *Pronotal surface sculpturing* (Fig. 35): Punctate; pits shallow, spaced closely together, each associated with a single long, narrow seta. *Scutellum* (Fig. 3): Relatively short, weakly produced anteriorly, with emarginate apex. *Legs* (Fig. 4): Tibiae foliaceous in some species; metathoracic femur without dorsal row of cucullate setae, tibiae with cucullate setae in enlarged setal row II (and, rarely, III); cucullate setae absent from row I. *Forewing* (Figs. 5–6): Basal ⅓ coriaceous, distal ⅔ either hyaline or semi-translucent; vein R_{2+3} basally fused with R_1; 1 r-m and 1 m-cu crossvein present (location of crossvein differs between subgenera). *Genitalia:* ♀: 2nd valvulae (Fig. 7) slightly curved dorsally, of roughly uniform width, tapered apically; dorsal ridge of distal ½ usually with small serrations. ♂: Lateral plates fused to pygofer; aedeagus and styles (Fig. 8) relatively elongate; aedeagus tapered apically, anterior face of posterior arm with preapical area denticulate; styles of variable width, always with strongly hooked apices.

Late-instar nymph (Fig. 9).—Unknown for most species; pronotum laterally flattened, metopidium vertically produced into low median horn; tibiae foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 5–9, fringed with setae.

Range.—Argentina [AMNH]; Bolivia [USNM]; Brazil [NCSU]; Peru [USNM]; Ecuador [NCSU]; French Guiana[1]; Suriname [USNM]; Guyana [NCSU]; Venezuela [IZAV]; Trinidad [BMNH]; Colombia [USNM]; Panama [USNM]; Costa Rica [INBC]; Nicaragua[1]; Honduras[1]; Guatemala [USNM]; Mexico [USNM].

Material examined.—13 specimens from AMNH; 22 from BMNH; 8 from BPBM; 6 from CNCI; 8 from INBC; 25 from IZAV; 4 from MZLU; 67 from NCSU; 3 from QCAZ; 48 from SHMC; 15 from TKWC; 115 from USNM.

Remarks.—Sakakibara (1972b) published a major revision of *Lycoderes,* including descriptions and illustrations of most species (excluding those not occurring in Brazil), as well as a taxonomic key. We present the description of a new species, a checklist of described *Lycoderes* species (listing synonymies and new subgeneric placements), a modified translation of Sakakibara's key (originally published in Portuguese), and selected new illustrations for descriptive purposes. Several *Lycoderes* species were not examined during this work, and so we present the modified translation of Sakakibara's dichotomous key rather than a novel, comprehensive key. *Lycoderes* exhibits a relatively high degree of sexual dimorphism, often making species identification difficult; although Sakakibara's treatment alleviated much of this confusion, further work remains to determine the status of species that were omitted or new since his contribution. Reference to Sakakibara's figures (1972b) is recommended when identifying specimens of *Lycoderes* to the species level.

The subgenera *Lycoderides* and *Lycoderes* are defined by the shape of cell M_{1+2} (the fourth apical cell of the forewings; Figs. 5–6, respectively), although it is the placement of the r-m crossvein in relation to the fork of vein M that determines the cell's shape. Several species previously unplaced in the genus *Lycoderes* are here assigned to either the subgenus *Lycoderides* Sakakibara (r-m crossvein either basad of, or at, the fork of vein M) or *Lycoderes* Germar (r-m crossvein distad of the fork of vein M). Included in the subgenus *Lycoderides* are: *L. fernandezi* Strümpel (1988a: 147), *L. luteus* Funkhouser (1940a: 275), *L. phasianus* Fowler (1896e: 164), and *L. serraticornis* Fowler (1896e: 165); included in

the subgenus *Lycoderes* are: *L. capitatus* Buckton (1903a: 203) and *L. minamen* (Buckton) (1903b: 51).

The immature stages are unknown for most *Lycoderes* species; those that are known appear very similar to the nymphs of the closely related genus *Stegaspis,* differing primarily in their less foliaceous tibiae (Figs. 9, 34). Host plant information is limited to the following: Richter (1942c) reported *L. serraticornis* on *Bellucia* sp. (family Melastomataceae) and *L. petasus* from an unspecified species of the same family; Haviland (1925a) collected *L. hippocampus* on unidentified low shrubs in "shaded places," noting the absence of ant attendants; Wood (1984a) reported *L. phasianus* from *Miconia* sp. (Melastomataceae); McKamey (pers. comm.) collected *Lycoderes* from *Vismia* sp. (Guttiferae).

The Greek generic name, "*Lycoderes,*" translates as "wolf neck," probably comparing the enlarged pronotal metopidium to the hackles on a canine neck. When making a generic name that refers to a feature of the prothorax, it is customary to modify the Greek noun "*dere*" to "*deres,*" thereby making the name masculine (W. Kuschel, personal communication). Therefore, the names of *Lycoderes* species should have masculine endings, unless the name is a noun in opposition.

Lycoderes (Lycoderides) nathanieli Cryan, new species
(Figs. 10–15)

Type locality.—Sierrazul, Napo Province, Ecuador.

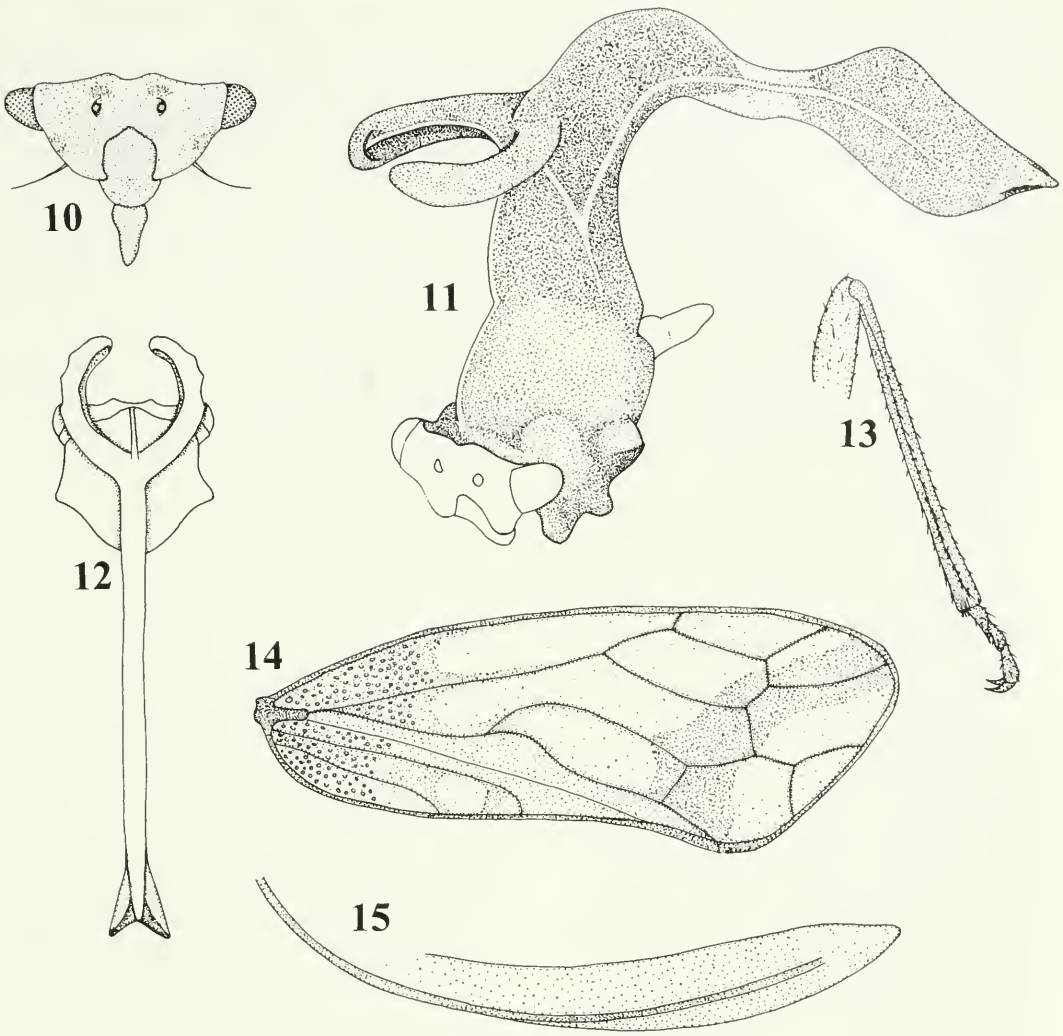
Diagnosis.—*Lycoderes nathanieli* has enlarged suprahumeral horns extending anteriorly and curving toward the midline; the elevated posterior pronotal process bears two small pyramiform 'horns' apically; metathoracic tibia with reduced cucullate setae in rows II and III.

Adult (♀).—*Dimensions* (mm): Total length 9.9; width between humeral angles 2.3; pronotal length 7.2; forewing length 8.2; maximum width of head across eyes 2.1. *Coloration:* Pronotum generally dark brown with lighter metopidium; constriction in posterior pronotal process tan; scutellum with dark brown anterior base and pale apex; forewings hyaline with darker basal and apical pigmentation. *Structure: Head:* Face (Figs. 10–11) with fine pubescence; ocelli on centro-ocular line; dorsal projections small, nearly indistinguishable, with apices separated by a distance just shorter than the distance between ocelli. *Thorax: Pronotum* (Figs. 11–12): Middorsal ridge slightly produced, extending over full length of pronotum; supraocular callosities distinct; humeral angles moderately produced; pronotum raised vertically, with suprahumeral horns and posterior process well above body and a slightly raised carina on each side, extending both anteriorly and posteriorly; suprahumeral horns extending horizontally and anteriorly, curving inward, apices nearly meeting to approximate a circle; posterior process extending to end of abdomen, laterally compressed, with semi-constricted median area; apex of posterior process with one pyramiform, lateral projection on each side. *Scutellum* (Fig. 11): Relatively short; slightly produced for entire length (anterior region raised higher); apex acuminate. *Legs* (Fig. 13): Metathoracic femur lacking dorsal row of cucullate setae; metathoracic tibia with three enlarged setal rows: setal row I lacking cucullate setae, rows II and III with few, very reduced cucullate setae only on distal halves of produced ridges. *Forewing* (Fig. 14): Basal ¼ slightly thickened, punctate except for area between vein Cu and claval suture; 1 r-m and 1 m-cu crossvein. *Genitalia* (Fig. 15): 2nd valvulae relatively uniform in width and slightly curving dorsally; dorsal ridge lacking serration. ♂: Unknown.

Late-instar nymph.—Unknown.

Distribution.—Ecuador: Napo Province.

Material examined.—*Holotype:* [♀, dissected] from Escuela Politecnica Nacional, Quito, Ecuador (on indefinite loan to



Figs. 10–15. *Lycoderes nathanieli,* structures of the holotype. 10, Head, anterior aspect (face). 11, Head, pronotum, and scutellum, anterolateral aspect. 12, Head and pronotum, dorsal aspect. 13, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 14, Right forewing. 15, Female second valvulae, lateral aspect.

USNM), with labels "ECUADOR: Napo Prov./Sierrazul, 2,200 m/SW of Baeza/O 40′S 77 55′W 22–30/Jan. 1996, T. J. Henry" and "Holotype / *Lycoderes/nathanieli/* J. R. Cryan."

Remarks.—The pronotal structure of *L. nathanieli* is unusual in that the metopidium and posterior pronotal process are similar to those of other *Lycoderes* (and even *Stegaspis*) species, but the suprahumeral horns are reminiscent of those of *Oeda informis* and *O. hamulata,* albeit much more produced. Unlike most other species of *Lycoderes,* the metathoracic tibiae of *L. nathanieli* bear reduced cucullate setae in the distal halves of setal rows II and III. Position of the r-m crossvein (basad of the fork of vein M) places *L. nathanieli* in the subgenus *Lycoderides.*

This species is named for Nathaniel Cryan, who was born during the preparation of this publication.

Partial Key to Subgenera and Species of Adult *Lycoderes* (Modified from Sakakibara 1972b)

1. Forewing (Fig. 5) with r-m crossvein basad of, or at, fork of vein M; cell M_{1+2} transverse, more or less triangular; Subgenus *Lycoderides* Sakakibara 2
– Forewing (Fig. 6) with r-m crossvein distad of fork of vein M; cell M_{1+2} not transverse, more or less trapezoidal; Subgenus *Lycoderes* Germar 7
2. Pronotum with suprahumeral horns long, or at least contiguous 3
– Pronotum with suprahumeral horns much shortened, situated laterally, with slightly elevated longitudinal, median carina between them (Fig. 2) 5
3. Suprahumeral horns extending anteriorly from pronotum, curving in towards midline . . . . . *L. nathanieli* Cryan, new species
– Suprahumeral horns variable, not as above 4
4. Suprahumeral horns contiguous; posterior pronotal process nearly straight, its lower basal portion very close to scutellum; forewing with one small, triangular, hyaline area adjoining costal margin, occupied by cell R_1 and cell R_{2+3}, the discoidal cell, and a small part of costal area . . . . . *L. burmeisteri* Fairmaire
– Suprahumeral horns divergent; posterior pronotal process slightly sinuous, its lower basal portion more remote from scutellum; forewing with one large, triangular, hyaline area adjoining costal margin, with discoidal cell in its center *L. fuscus* Amyot and Serville
5. Pronotal process strongly elevated, subcylindrical; posterior process extending horizontally from the posteromedial portion of pronotal cylinder, curving basally and after, backwards at an angle, straight, shaped like steps of a staircase . . . . . *L. gradatus* Sakakibara
– Pronotal process not much elevated, more or less constricted; slightly sinuate posterior process originating subapically or basally (on pronotal process) and extending over abdomen (Fig. 2) 6
6. Each suprahumeral horn, viewed from above, triangular, much longer than its basal width . . . . . *L. hippocampus* (Fabricius)
– Each suprahumeral horn, viewed from above, rounded, shorter than its basal width *L. amazonicus* Sakakibara, *L. brevilobus* Sakakibara
7. Male 8
– Female 23
8. Apices of suprahumeral horns separated by a distance greater than 2× maximum length of head 9
– Apices of suprahumeral horns separated by a distance much less than 2× maximum length of head 12
9. Suprahumeral horns basally inflated, basal width greater than width between humeral angles; in anterior view, the contour line of the pronotal arch more or less in form of a half-moon . . . . . *L. mitratus* Germar
– Suprahumeral horns not inflated, basal width much smaller than width between humeral angles (Fig. 3); in anterior view, space between suprahumeral horns concave 10
10. Forewing ferrugineous, with one transverse, translucent median band; posterior pronotal process sickle-shaped . . . *L. furcifer* Sakakibara
– Forewing dark chestnut in color, with one hyaline area adjoining costal margin; posterior pronotal process nearly adjoining scutellum along its outline (contour) 11
11. Forewing with hyaline area distinctly triangular . . . . . *L. reichardti* Sakakibara
– Forewing with hyaline area elongate, more or less shaped like a half-moon . . . . . *L. apertus* (Walker)
12. Forewing entirely dark 13
– Forewing with one transverse band or one nearly hyaline median area 14
13. Pronotum strongly elevated above head, reaching a height nearly equal to its length, in lateral view L-shaped . . . . . *L. fabricii* Metcalf and Wade
– Pronotum regularly elevated above head, reaching a height just greater than half its length, in lateral view more or less triangular . . . . . *L. unicolor* Fairmaire
14. Forewing with a round, median, hyaline area; frontal view with pronotum swollen at apex . . . . . *L. clavatus* Sakakibara
– Forewing with a transverse hyaline band; frontal view with pronotum not swollen at apex 15
15. Base of posterior pronotal process removed from scutellum by a distance equal to or greater than its length 16
– Base of posterior process adjoining or slightly removed from scutellum 19
16. Apex of posterior pronotal process reaching inner angle of forewing; abdomen orange colored . . . . . *L. ancora* (Germar)
– Apex of posterior pronotal process not reaching inner angle of forewing; abdomen ashen or chestnut colored 17
17. Apices of suprahumeral horns separated by a distance approximately equal to width between humeral angles; posterior pronotal process constricted; forewing widened at apex, with external angles straight . . . . . *L. gladiator* Germar
– Apices of suprahumeral horns separated by a

distance less than width between humeral angles; posterior process with basal half subcylindrical; forewing more or less narrowed, with external angle acute 18

18. Anterior face of pronotum elevated vertically above head . . . . . *L. alvarengai* Sakakibara
– Anterior face of pronotum elevated obliquely above head . . . . . *L. wygodzinskyi* Sakakibara

19. Posterior pronotal process thin, basal width about 0.2× its length . . . . *L. petasus* Fairmaire
– Posterior pronotal process compressed, basal width greater than 0.3× its length 20

20. Apical spot of forewing with small hyaline area adjoining distal margin 21
– Apical spot of forewing without small hyaline area 22

21. Apices of suprahumeral horns separated by a distance slightly greater than interocular distance; outline of pronotum slightly sinuate . . . . . *L. gaffa* Fairmaire
Apices of suprahumeral horns separated by a distance about 0.5× interocular distance; outline of pronotum slightly arched . . . . . *L. foliatus* Sakakibara

22. Tibiae with 3 dark, transverse bands . . . . . *L. luctans* Stål
– Tibiae without dark, transverse bands . . . . . *L. turritus* Sakakibara

23. Suprahumeral horns strongly divergent, distance between their apices greater than 2× width between the humeral angles 24
– Suprahumeral horns more or less contiguous, or if divergent, distance between apices less than width between humeral angles 27

24. Posterior pronotal process sickle-shaped; suprahumeral horns V-shaped 25
– Posterior pronotal process not sickle-shaped; suprahumeral horns horizontal or slightly curved basally 26

25. Posterior pronotal process reaching apex of clavus; forewing hyaline with dark apical spot . . . . . *L. ancora* (Germar)
– Suprahumeral horns not inflated, basal width approximately equal to 0.5× width between humeral angles; anterior view with pronotal outline depressed in middle . . . . . *L. reichardti* Sakakibara

26. Posterior pronotal process distinctly sickle-shaped, with an average diameter of space between posterior pronotal process and scutellum greater than greatest diameter of eyes; forewing yellowish ferrugineous, generally with somewhat distinct apical spot 28
– Posterior pronotal process not sickle-shaped, that is, adjoining scutellum or, when separated, with an average diameter of space less than greatest diameter of eyes; forewing dark or with very distinct apical spot 30

27. Suprahumeral horns slightly longer than interocular distance, with points slightly divergent, turning toward front in approximate horizontal plane of posterior pronotal process . . . . . *L. gladiator* Germar
– Suprahumeral horns approximately 2× interocular distance, contiguous but turning out toward top, points much higher than horizontal plane of posterior pronotal process 29

28. Anterior of pronotum undulating; color generally yellowish ferrugineous, with coxae, head, and anterior portion of pronotum dark chestnut; forewing with apical spot very weakened, nearly imperceptible . . *L. luctans* Stål
– Anterior of pronotum nearly straight; color generally chestnut ferrugineous; forewing with apical spot more or less distinct . . . . . *L. gaffa* Fairmaire

29. Forewing entirely dark or slightly translucent in middle 31
– Forewing with large, conspicuous hyaline area 32

30. Distance from humeral angles to bases of suprahumeral horns more than length of posterior pronotal process; suprahumeral horns short and divergent . . . . . *L. fabricii* Metcalf and Wade
Distance from humeral angles to base of suprahumeral horns less than length of posterior process; suprahumeral horns more or less long and contiguous . . . . *L. unicolor* Fairmaire

31. Posterior pronotal process long, its basal width about 0.5× its length 32
– Posterior pronotal process thin, its basal width about 0.2× its length 33

32. Pronotal outline triangular in lateral view, with dorsal angle nearly straight; dorsal outline more or less arched . . . . . *L. unicolor* Fairmaire
– Pronotal outline triangular in lateral view, with dorsal angle pointed; dorsal outline slightly sinuate . . . . . *L. turritus* Sakakibara

33. Color of posterior pronotal process uniform, adjoining scutellum or slightly removed, but not by more than its basal width; suprahumeral horns generally contiguous . . . . . *L. petasus* Fairmaire
– Color of posterior pronotal process paler basally, removed from scutellum by a distance greater than its basal width; suprahumeral horns generally divergent 34

34. Pronotum, in lateral view, projecting obliquely anteriorly; suprahumeral horns nearly equal in length to interocular distance . . . . . *L. wygodzinskyi* Sakakibara
– Pronotum, in lateral view, not projecting obliquely anteriorly, anterior portion more or less vertical; suprahumeral horns nearly equal

in length to 0.3× interocular distance . . . . . *L. alvarengai* Sakakibara

Species Checklist of *Lycoderes*

Subgenus *Lycoderides* Sakakibara 1972b: 92. Type-species: *Centrotus hippocampus* Fabricius 1803a, by original designation.

amazonicus Sakakibara
Lycoderes amazonica Sakakibara 1991a: 655.

brevilobus Sakakibara
Lycoderes brevilobus Sakakibara 1972b: 102.

burmeisteri Fairmaire
Lycoderes burmeisteri Fairmaire 1846b: 525.
Enchenopa laeta Walker 1851a: 494.
Enchenopa fissa Walker 1851b: 685.
Lycoderes igniventer Buckton 1903a: 200.
Lycoderes triangulata Funkhouser 1919c: 27.

cultratus Sakakibara
Lycoderes cultrata Sakakibara 1991a: 657.

fernandezi Strümpel, **new subgeneric placement**
Lycoderes fernandezi Strümpel 1988a: 147.

fuscus Amyot and Serville
Lycoderes fuscus Amyot and Serville 1843a: 561.
Lycoderes angustata Buckton 1903a: 201.
Lycoderes fusca: Metcalf and Wade 1965a: 56.

gradatus Sakakibara
Lycoderes gradatus Sakakibara 1972b: 101.

hippocampus (Fabricius)
Centrotus hippocampus Fabricius 1803a: 20.
Lycoderes pileolum Fairmaire 1846b: 526.
Lycoderes hippocampus: Walker 1851a: 634.
Lycoderes hippocampa: Metcalf and Wade 1965a: 59.

luteus Funkhouser, **new subgeneric placement**
Lycoderes luteus Funkhouser 1940a: 275.
Lycoderes lutea: Metcalf and Wade 1965a: 61.

marginalis (Walker)
Membracis marginalis Walker 1851a: 479.
Stegaspis marginalis: Metcalf and Wade 1965a: 73.
Lycoderes marginalis: Sakakibara 1991a: 652.

nathanieli Cryan, **new species**

obtusus Sakakibara
Lycoderes obtusa Sakakibara 1991a: 657.

pennyi Sakakibara
Lycoderes pennyi Sakakibara 1991a: 653.

phasianus Fowler, **new subgeneric placement**
Lycoderes phasianus Fowler 1896e: 164.
Lycoderes phasiana: Metcalf and Wade 1965a: 62.

protensus Sakakibara
Lycoderes protensa Sakakibara 1991a: 659.

serraticornis Fowler, **new subgeneric placement**
Lycoderes serraticornis Fowler 1896e: 165.

strumpeli Sakakibara
Lycoderes strumpeli Sakakibara 1991a: 653.

Subgenus *Lycoderes* Germar 1835a.
Corythophora Stål 1869a: 53.
Lophucha Stål 1869a: 54.
Rhyparoptera Stål 1869a: 54.

alvarengai Sakakibara
Lycoderes alvarengai Sakakibara 1972b: 131.

ancora (Germar)
Centrotus ancora Germar 1821a: IV.32.
Bocydium galeritum Lesson 1832a: 56.
Lycoderes ancora: Germar 1835a: 259.
Lycoderes furca Fairmaire 1846b: 524.
Lycoderes galeritus: Fairmaire 1846b: 523.

Lycoderes lobatus Stål 1862e: 34.
Lycoderes wahlbergi Stål 1862e: 35.
Corythophora galerita: Buckton 1903a: 267.
Lycoderes galerita: Metcalf and Wade 1965a: 57.

apertus (Walker)
Enchenopa aperta Walker 1858c: 337.
Guayaquila aperta: Funkhouser 1927f: 36.
Stegaspis aperta: Goding 1928a: 395.
Lycoderes apertus: Sakakibara 1972b: 111.

argutus Sakakibara
Lycoderes arguta Sakakibara 1991a: 661.

capitatus Buckton, **new subgeneric placement**
Lycoderes capitata Buckton 1903a: 203.

clavatus Sakakibara
Lycoderes clavatus Sakakibara 1972b: 123.

fabricii Metcalf and Wade
Membracis emarginata Fabricius 1803a: 14.
Membracis flexuosa Fabricius 1803a: 16; nomen novum for *Membracis emarginata* Fabricius 1803a [nec *Membracis emarginata* Fabricius 1798a].
Lycoderes emarginatus: Stål 1869a: 53.
Rhyparoptera emarginata: Buckton 1903a: 270.
Lycoderes fabricii Metcalf and Wade 1965a: 55; nomen novum for *Membracis flexuosa* Fabricius 1803a [nec *Membracis flexuosa* Fabricius 1794a].

foliatus Sakakibara
Lycoderes foliatus Sakakibara 1972b: 124.

furcifer Sakakibara
Lycoderes furcifer Sakakibara 1970b: 25.

gaffa Fairmaire
Lycoderes gaffa Fairmaire 1846b: 524.
Centrotus latipennis Walker 1851a: 607.
Stegaspis bellicosa Walker 1858b: 165.
Lycoderes latipennis: Stål 1862b: 491.
Pterygia subminax Walker 1862a: 316.
Stegaspis latipennis: Buckton 1903a: 270.
Lophucha gaffa: Buckton 1903a: 268.

gladiator Germar
Lycoderes gladiator Germar 1835b: 310.
Lycoderes corniger Stål 1862e: 36.
Lycoderes torta Buckton 1903a: 202.
Lycoderes fuscata Buckton 1903a: 204.

luctans Stål
Lycoderes luctans Stål 1862e: 35.

minamen (Buckton), **new subgeneric placement**
Enchenopa minamen Buckton 1903b: 51.
Lycoderes minamen: Funkhouser 1927f: 436.

mitratus Germar
Lycoderes mitratus Germar 1835b: 311.
Lycoderes spinolae Fairmaire 1846c: 12.
Lycoderes mitrata: Metcalf and Wade 1965a: 62.

petasus Fairmaire
Lycoderes petasus Fairmaire 1846b: 526.
Lycoderes petasa: Metcalf and Wade 1965a: 62.

reichardti Sakakibara
Lycoderes reichardti Sakakibara 1972b: 109.

turritus Sakakibara
Lycoderes turritus Sakakibara 1970b: 27.

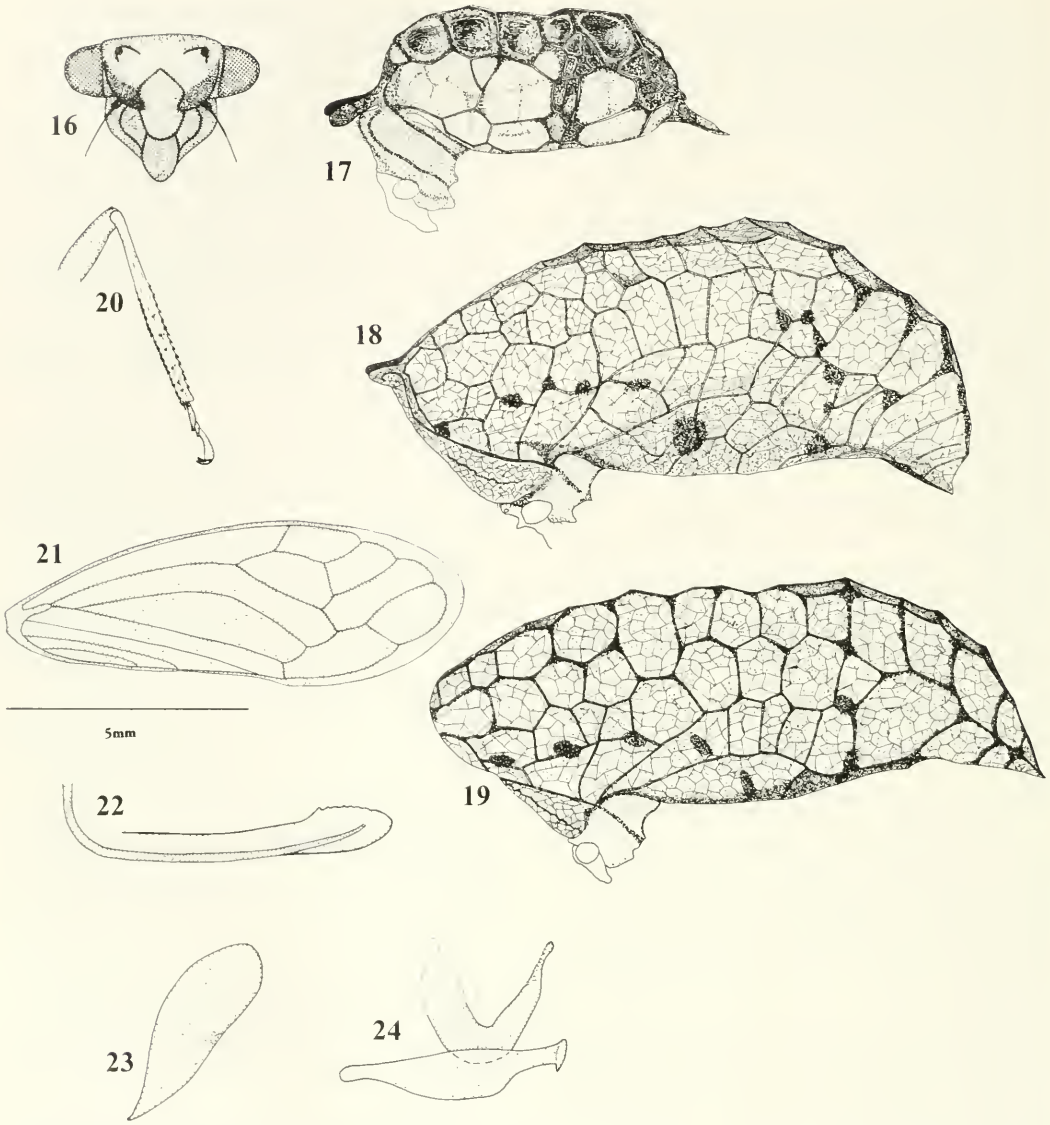
unicolor Fairmaire
Lycoderes unicolor Fairmaire 1846b: 526.
Stegaspis insolita Walker 1858b: 109.
Lycoderes prolixus Stål 1862e: 35.
Lycoderes truncatulus Stål 1862e: 36.
Lycoderes truncatulis Buckton 1903a: 203.
Lycoderes insolita: Metcalf and Wade 1965a: 60.

wygodzinskyi Sakakibara
Lycoderes wygodzinskyi Sakakibara 1972b: 129.

Genus *Oeda* Amyot and Serville, 1843a

Oeda Amyot and Serville 1843a: 546. Type species: *Membracis inflata* Fabricius 1787a, by original designation.
Aeda [sic] Spinola 1850a: 55.
Ada [sic] Desmarest 1859a: 199.

Diagnosis.—*Oeda* differs from other stegaspidine genera in the balloon-like infla-



Figs. 16–24. *Oeda* species. 16, *O. inflata,* head, anterior aspect (face). 17–19, Head and pronotum, anterolateral aspect of *O. informis, O. hamulata,* and *O. inflata,* respectively. 20, *O. informis,* left metathoracic femur, tibia, and tarsus, ablateral aspect. 21, *O. hamulata,* right forewing. 22, *O. inflata,* female second valvulae, lateral aspect. 23, *O. informis,* male left lateral plate, lateral aspect. 24, *O. informis,* male aedeagus and left style, lateral aspect.

tion of the posterior pronotal process, which has well defined and reticulate venation.

Adult.—*Dimensions* (mm): Total length 7.5–13.8. *Structure: Head* (Fig. 16): Dorsal projections either absent or very small; ocelli on raised tubercles; foliate lobes extend over postclypeus. *Thorax: Pronotum* (Figs. 17–19): Suprahumeral horns (if present) short, simple; posterior pronotal process long, inflated, variously reticulate. *Pronotal surface sculpturing* (Fig. 36): Metopidium punctate; pits small, spaced regularly, not associated with a seta; posterior process membranous, not punctate. *Scutel-*

lum: Short, moderately elevated anteriorly; apex broadly acuminate (rounded). *Legs* (Fig. 20): Metathoracic femur lacking cucullate setae, tibiae with cucullate setae in rows II and III. *Forewing* (Fig. 21): Apical limbus wide; vein R_{2+3} fused basally with R_1; 1 r-m and 1 m-cu crossvein present (crossvein r-m remotely basad of fork of vein M). *Genitalia:* ♀: 2nd valvulae (Fig. 22) basal ⅔ slender, distal ⅓ broadened with dorsal serrations. ♂: lateral plates (Fig. 23) free, without apical hook; aedeagus and styles (Fig. 24) relatively short, stout; styles hooked apically; aedeagus tapering apically, anterior face of posterior arm with preapical area weakly denticulate.

Late-instar nymph.—Unknown for all species.

Range.—Argentina[3]; Paraguay [NCSU]; Bolivia [USNM]; Peru [AMNH]; Ecuador [MZLU]; Brazil [AMNH]; French Guiana[1]; Suriname[1]; Guyana[1]; Venezuela [IZAV]; Colombia [USNM]; Costa Rica [TKWC].

Material examined.—Type specimens not examined. Other specimens: *O. hamulata:* 1 ♂ from AMNH, 1 ♀ from IZAV, 4 ♀ from NCSU, 1 ♀ from SEMC, 5 ♀ from USNM (including Cryan Research #93-162a ♀), 3 ♀ from ZMUH. *O. inflata:* 1 ♀ from AMNH, 1 ♀ from MZLU, 1 ♀ from TKWC, 2 ♀ from USNM (including Deitz Research #71-293a ♀), 3 ♀ from ZMUH. Sp. possibly *O. mirandai*: 5 ♀ from ZMUH. *O. informis*: 3 ♀ from AMNH, 2 ♀ from NCSU, 1 ♀ from SEMC, 1 ♂ from SHMC (Cryan Research #94-299a ♂), 4 ♀ from USNM (including Cryan Research #94-300b ♀).

Remarks.—The genus *Oeda* was revised by Fonseca (1951a), who erected the new subgenus *Oedacanthus* and recognized four species. These species are some of the strangest, most bizarre treehoppers known. Aside from the illustrations presented in this work (Fig. 28), drawings of *O. hamulata* were given by Vignon (1930a), Seitz (1951a), Fonseca (1951a), and Richter (1955a, with a discussion of pronotal evolution theories). Schröder (1962a), Boulard (1986a), and Klausnitzer (1987a) all published pictures of *O. hamulata* (as *O. inflata* in the figure captions). *Oeda informis* was illustrated by Vignon (1930a), Fonseca (1951a), and Richter (1955a). Wood (1984a) reported that three adults of *O. inflata* were collected from one leaf of *Cecropia* sp. (Moraceae). Nymphs of all species of *Oeda* remain unknown.

Deitz's (1975a) statement that the male lateral plates are absent in *Oeda* seems to be incorrect. The lateral plates are present and free (no apical hooks) in *O. informis* (Fig. 23) and *O. hamulata,* resembling the lateral plates of the closely related genus *Bocydium* (Cryan and Deitz 1999a). Males of *O. inflata* and *O. mirandai* were not examined, but are presumed to have lateral plates.

The type specimen of *O. mirandai* was not examined. Based on the original description, the difference between this species and *O. hamulata* seems to lie solely in the relative lengths of their balloon-like posterior pronotal processes. Some specimens examined in this work have pronota like *O. hamulata,* except the suprahumeral horns are reduced to mere nubs. If these specimens represent *O. mirandai,* then there is no doubt about that species' validity. Although *O. mirandai* is recognized here as a separate species, it may not actually be valid.

The purpose of the inflated posterior pronotal process is unknown. Rietschel (1987a) suggested that this bizarre structure serves as a "passive protecting adaptation," specialized against predators (e.g. birds and lizards) that attack the pronotum. Following this theory of autotomy, the predator grasps the inflated pronotum, which apparently breaks along a "fault-line" located at the base of the posterior process where the diameter is smallest, thus allowing the insect to escape. Unlike the pronotal fault-line visible in the genus *Anchistrotus* Buckton of the subfamily Heteronotinae (Boulard 1983a), however, the fault-line is not plainly visible in *Oeda.* Buckton (1903b) hy-

pothesized that the pronotum of *Oeda* mimics fragments of dead leaves in their yellow-orange color, their leaflike venation, and their small, dark spots that might correspond to sites where insect feeding has damaged a leaf surface. A theory proposed by Poulton (in Buckton 1903b), suggested that this structure mimics the empty pupal case of some Neotropical butterflies and moths. Finally, T. K. Wood (personal communication) has speculated that this mysterious structure may play some role in thermoregulation or in sound reverberation.

The generic name is based on the Greek noun "oidema," meaning "a swelling."

Key to Subgenera and Species of Adult *Oeda*

(Modified from Fonseca 1951a)

1. Swollen pronotal process sessile (Figs. 18–19) and opaque, with finely reticulate areas; posterior pronotal process unarmed apically; Subgenus *Oeda* Amyot and Serville 2
– Swollen pronotal process pedunculate (Fig. 17) and translucent, glassy, without finely reticulate areas; posterior pronotal process with spiny (thornlike) apical projection; Subgenus *Oedacanthus* da Fonseca ..... *O. informis* (Westwood)
2. Anterior of pronotal swelling with two digitate suprahumeral horns (Fig. 18) 3
– Anterior of pronotal swelling without digitate suprahumeral horns (Fig. 19) ..... *O. inflata* (Fabricius)
3. Posterior pronotal process extending beyond wing apices (at rest) ..... *O. hamulata* Stål
– Posterior pronotal process not extending beyond wing apices .... *O. mirandai* da Fonseca

Species Checklist of *Oeda*

Subgenus *Oeda* Amyot and Serville 1843a.

hamulata Stål

Oeda hamulata Stål 1869a: 52.

inflata (Fabricius)

Membracis inflata Fabricius 1787a: 262.

Cicada inflata: Linnaeus 1790: 2092.

Smilia inflata: Germar 1833a: 177.

Oeda inflata: Amyot and Serville 1843a: 547.

Oeda inermis: Fairmaire 1846b: 506.

Oeda frondosa: Buckton 1903a: 206.

mirandai Fonseca

Oeda mirandai Fonseca 1951a: 211.

Subgenus *Oedacanthus* Fonseca 1951a: 211. Type-species: *Smilia informis* Westwood 1842a, by original designation.

informis (Westwood)

Smilia informis Westwood 1842a: 119.

Oeda informis: Fairmaire 1846b: 507.

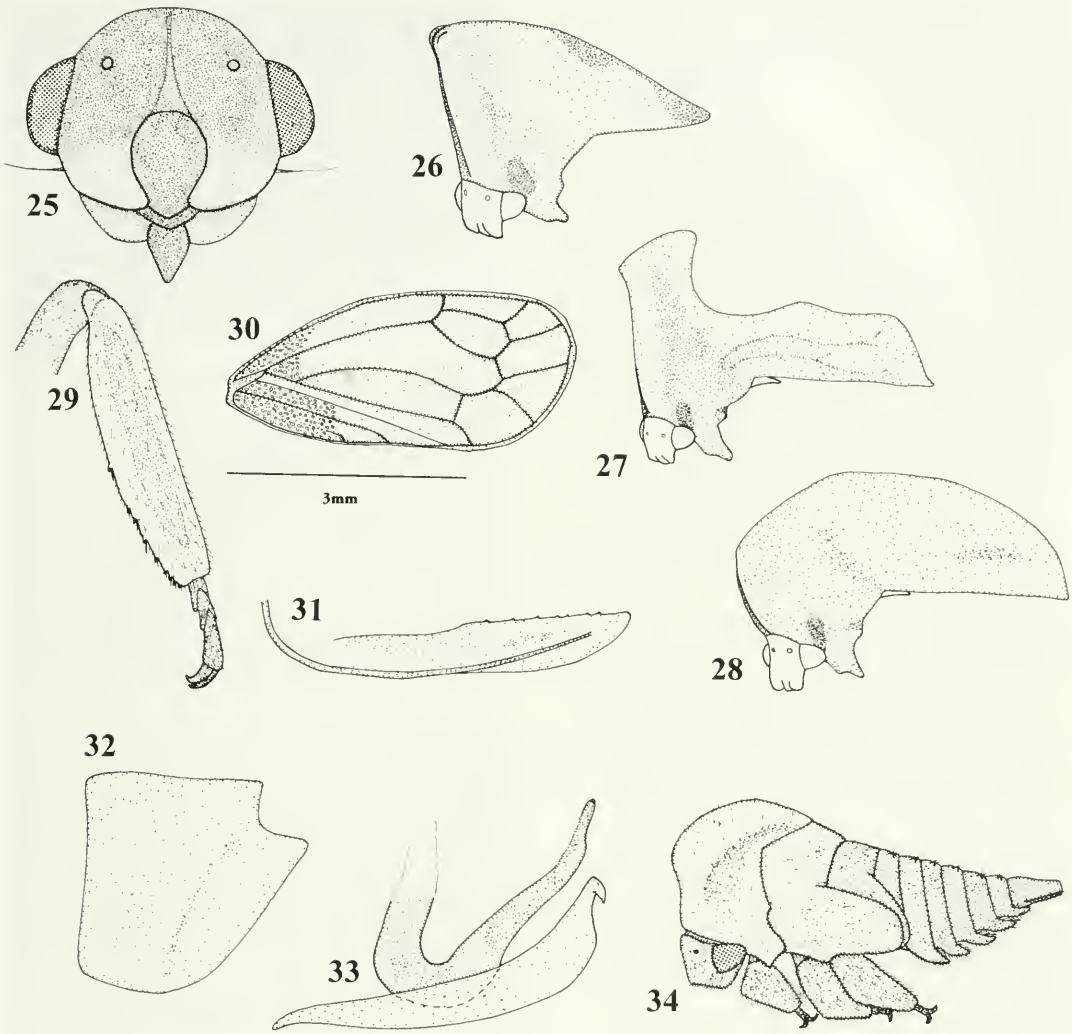
Genus *Stegaspis* Germar, 1833a

Stegaspis Germar 1833a: 177. Type species: *Cicada fronditia* Linnaeus 1758a, by subsequent designation of Kirkaldy 1901e: 219.

Membracis Fabricius: Blanchard 1840a: 180 [error].

Diagnosis.—*Stegaspis* is unique among Stegaspidini in having the foliate lobes of the head extending over the postclypeus.

Adult.—*Dimensions* (mm): Total length 5.6–7.7. *Structure: Head* (Fig. 25): Finely setose; dorsal projections absent; foliate lobes rounded, extending over unilobed postclypeus. *Thorax: Pronotum* (Figs. 26–28): Metopidium elevated, laterally compressed; suprahumeral horns absent (or, at most, represented by extremely small carinae at metopidial apex); posterior process foliaceous, either dorsally or completely concealing scutellum. *Pronotal surface sculpturing* (Fig. 37): Punctate; pits shallow and closely spaced, each associated with a single long, narrow seta. *Scutellum* (Figs. 27–28): Relatively short, weakly produced anteriorly, with emarginate apex. *Legs* (Fig. 29): Tibiae strongly foliaceous; metathoracic femur without dorsal row of cucullate setae, tibia with cucullate setae in row II only. *Forewing* (Fig. 30): Basal ⅓ coriaceous, distal ⅔ hyaline; vein R_{2+3} basally fused with R_1; 1 r-m and 1 m-cu crossvein present (r-m crossvein distad of fork of vein M). *Genitalia:* ♀: 2nd valvulae (Fig. 31) roughly uniform in width, tapered apically; dorsal ridge of distal ½ with small serrations. ♂: Lateral plates fused to pygofer (Fig. 32); aedeagus and styles (Fig. 33) elongate; aedeagus tapered apically, anterior face of posterior arm with preapical



Figs. 25–34. *Stegaspis* species. 25, *S. bracteata,* head, anterior aspect (face). 26–28, Head, pronotum, and scutellum, anterolateral aspect of *S. bracteata, S. fronditia* (female), and *S. fronditia* (male), respectively. 29, *S. bracteata,* left metathoracic femur, tibia, and tarsus, ablateral aspect. 30, *S. bracteata,* right forewing. 31, *S. fronditia,* female second valvulae, lateral aspect. 32, *S. fronditia,* male left lateral plate and pygofer, lateral aspect. 33, *S. fronditia,* male aedeagus and left style, lateral aspect. 34, *S. bracteata,* late-instar nymph, lateral aspect.

area weakly denticulate; styles of variable width, always with strongly hooked apices.

Late-instar nymph (Fig. 34).—Pronotum laterally flattened, metopidium vertically produced into low median horn; tibiae strongly foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 4–8, fringed with setae.

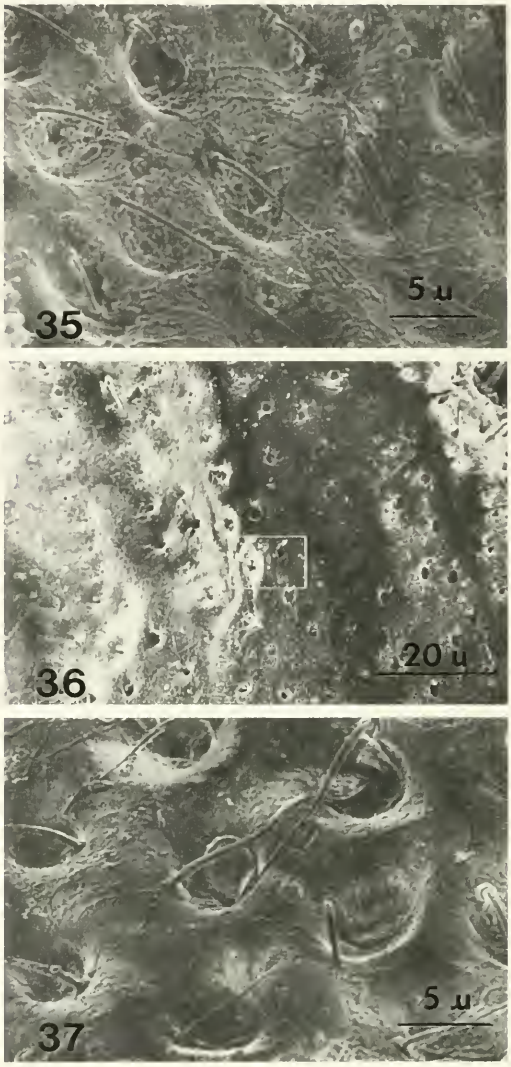
Range.—Bolivia [USNM]; Peru [NCSU]; Ecuador [QCAZ]; Brazil [USNM]; French Guiana[1]; Guyana [NCSU]; Suriname[2]; Venezuela [IZAV]; Trinidad [USNM]; Colombia [USNM]; Panama [USNM].

Material examined.—*Stegaspis bracteata* (Fabricius): Holotype of *Stegaspis viridis* Funkhouser [♀] [USNM], with labels: "Port of Spain/Trinidad, W.I./R.J. Crew," "WDFunkhouser/Collection/1962," and "TYPE/Stegaspis viridis." *Other specimens:* 1 ♂ from AMNH; 19 ♀, 30 ♂, 4

unknown (abdomens missing) from CNCI; 14 ♀, 19 ♂ from EMUS; 14 ♀, 19 ♂ from IZAV; 2 ♀, 6 ♂, 3 nymphs from SHMC; 1 ♂ from UCDC; 14 ♀, 10 ♂, 1 nymph from USNM. *Stegaspis fronditia* Linnaeus: Types not examined. *Other specimens:* 3 ♀, 1 ♂ from AMNH; 1 ♀, 1 ♂ from BMNH; 2 ♀, 1 ♂ from BPBM; 2 ♀ from CNCI; 8 ♀, 2 ♂ from IZAV; 1 ♀, 7 ♂ from MZLU; 46 ♀, 24 ♂ from NCSU; 4 ♀, 1 ♂ from QCAZ; 10 ♀, 2 ♂ from SEMC; 19 ♀, 6 ♂, 3 nymphs from SHMC; 1 ♂ from TKWC; 20 ♀, 10 ♂ from USNM.

Remarks.—Boulard (1979g) synonymized *Stegaspis fronditia* and *S. laevipennis,* believing the latter species to have been described from the males of the former. Sakakibara (1991a) recently revised the genus *Stegaspis,* recognizing these as distinct species (although Sakakibara did not examine specimens of *S. laevipennis*). Photographs of *S. fronditia* (Linnaeus) and *S. bracteata* (Fabricius) were included in Sakakibara's paper, although *S. laevipennis* (Fairmaire) was not illustrated in any manner. The type material of *S. laevipennis* was not examined in our work, either; no clear illustrations or complete descriptions of this species exist in the literature, and we examined no specimens that could be identified definitively as *S. laevipennis.* Therefore, we follow Boulard's (1979g) synonymy.

Haviland (1925a) reported that *S. fronditia* (as *S. galeata*) can be found with ant attendants. She hypothesized that the unusual pronotal shapes of *S. galeata* mimic bits of dead leaves, also observing that the foliaceous tibiae serve to obscure the outline of the insects as they cling to tree branches and twigs. Haviland described *S. fronditia* (as *S. galeata*) as living in colonies attended by ant mutuals, whereas *S. laevipennis* (now *S. fronditia*) is a solitary species, not ant-attended. Substrate mediated vibrational signals have been recorded from females of *S. fronditia* (R. Cocroft, personal communication). Poulton (1891a) illustrated a nymph of *Stegaspis* sp. (the illustration was later reproduced by Heikertinger [1954a]), describing the nymph as a mimic of leaf-cutting ants, the pronotal shape resembling jagged pieces of leaves carried over the backs of the ants. It is probable, however, that this nymph was actually a species of the genus *Cymbomorpha,* subfamily Darninae, that was incorrectly identified (McKamey, personal communication).



Figs. 35–37. Pronotal surface sculpturing of Stegaspidini. 35, *Lycoderes* sp. 36, *Oeda infornis.* 37, *Stegaspis fronditia.*

Other illustrations of *Stegaspis* in previous literature include Vignon's (1930a) figure of a *Stegaspis* sp. nymph, Suchantke's

(1983a) of a *S. fronditia* adult, Strümpel's (1983a) photograph of *S. fronditia* (as "*S. insignis*" in the caption), and Boulard's (1979g) of *S. fronditia* adults (one male and one female). Richter (1955a) discussed the possibility that the expanded pronota of Membracidae originated as the dorsal fusion of prothoracic wings, illustrating both *Stegaspis* spp. and *Oeda* spp. as examples.

The only host records for *Stegaspis* (Haviland 1925a) describe the plants rather than identify them: *S. fronditia* [as *S. galeata*] was collected from unidentified green vines and shoots in "shaded places." *Stegaspis laevipennis* is reported from a "slender, straggling tree, common in open places, [and] had the twigs and undersides of the leaves covered with rusty brown powder." Haviland's host plant descriptions are apparently consistent with *Vismia* sp. (family Guttiferae), on which species of *Bocydium* and *Lycoderes* were also collected (McKamey, personal communication).

Species of *Stegaspis* can be easily separated from the morphologically similar species of *Lycoderes* by the form of the head's foliate lobes: *Stegaspis* has the foliate lobes extending over the postclypeus (Fig. 25), sometimes nearly touching each other; the foliate lobes of *Lycoderes* do not extend over the postclypeus (Fig. 1). *Stegaspis,* like *Lycoderes* and other stegaspidine genera, exhibits sexual dimorphism with respect to pronotal structure (Figs. 27–28).

The generic name is a combination of the Greek terms "*steg*" (from "*stego,*" meaning "roof or cover") and "*aspis*" (meaning "shield"), perhaps referring to the fact that the pronota of *Stegaspis* almost entirely cover (protect) the dorsal surfaces of these insects.

Key to Species of Adult *Stegaspis*

1. Pronotum foliaceous, L-shaped in females (Fig. 27) and ovoid in males (Fig. 28) . . . . . *S. fronditia* (Linnaeus)
– Pronotum triangular in both sexes; dorsal pronotal margin nearly straight (Fig. 26) . . . . . *S. bracteata* (Fabricius)

Species Checklist of *Stegaspis*

bracteata (Fabricius)
Membracis bracteata Fabricius 1787a: 263.
Cicada bracteata: Donovan 1820a: 2.
Thelia bracteata: Fairmaire 1846a: 309.
Stegaspis bracteata: Stål 1869a: 54.
Stegaspis viridis Funkhouser 1915e: 104.
Lycoderes viridis Strümpel 1988a: 148.
Stegaspis viridis: Sakakibara 1991a: 652.

fronditia (Linnaeus)
Cicada fronditia Linnaeus 1758a: 435.
Cicada foliatasinuosa De Geer 1773a: 208.
Membracis fronditia: Fabricius 1781a: 316.
Membracis folium Olivier 1792a: 668.
Membracis melanopetalus Olivier 1792a: 668.
Membracis abdominalis Fabricius 1803a: 15. [equals *Stegaspis fronditia*: Sakakibara 1991a: 652].
Stegaspis fronditia: Germar 1833a: 177.
Stegaspis folium: Germar 1833a: 177.
Lycoderes fronditia: Fairmaire 1846b: 526.
Enchenopa galeata Walker 1851a: 486.
Stegaspis galeata: Walker 1858c: 341.
Stegaspis melanopetala: Stål 1869a: 54.
Hypsoprora insignis Buckton 1901a: 59.
Stegaspis insignis: Funkhouser 1922a: 34. [equals *Stegaspis fronditia*: Sakakibara 1991a: 652].
Lycoderes laevipennis Fairmaire 1846b: 527.
Stegaspis laevipennis: Walker 1851a: 635. [equals *Stegaspis fronditia*: Boulard 1979g]

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LIFE HISTORIES OF LOTIC MAYFLIES (EPHEMEROPTERA) IN AN OZARK STREAM: INSTAR DETERMINATION AND VOLTINISM

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Abstract.—Life history studies were conducted on four commonly occurring species of mayflies from an Ozark stream in Missouri. A multivariate statistical technique, using a suite of ln-transformed body measurements of *Stenonema mediopunctatum* (McDunnough) (Ephemeroptera: Heptageniidae) nymphs, discerned at least nine instars during the sampling period. This technique provided greater resolution in discriminating among instars than using raw data or head capsule widths alone. Further, *S. mediopunctatum* was determined to be univoltine in these streams, as were *Caenis hilaris* (Say) and *C. latipennis* Banks (Ephemeroptera: Caenidae). *Tricorythodes curvatus* Allen (Ephemeroptera: Leptohyphidae) apparently was multivoltine.

Key Words: Ephemeroptera, life history, voltinism, instar

The shift in ecological research from descriptive natural history to more quantitative approaches requires that life history and life cycle information constitute a larger part of studies dealing with community-level processes (Rosenberg 1979); however, life histories of most species of aquatic insects are not known in detail (Richardson and Tarter 1976). This type of information is important for a better knowledge not only of the insects themselves, but of their distribution and ecology. Mayflies are an important component of aquatic ecosystems and the life histories must be determined in order to have a complete understanding of their functions in aquatic ecosystems (Kondratieff and Voshell 1980). Further, knowledge of the number of instars for each mayfly species or population, and how this information correlates with environmental factors, will lead to a better understanding of their biology (Fink 1982, 1984), especially when describing life histories, life cycles, or energy budgets (Benton and Pritchard 1988).

The nymphal lifespan of temperate mayflies varies from 7–13 days (Gray 1981) to approximately 2.5 yr, depending on the species and geographic location of the population (see Brittain 1982, Sweeney et al. 1995). Instar number, which is variable in mayflies (Brittain 1982, Fink 1982, 1984), ranges from 10 to 50, with most species in the range of 15–25 (see Brittain 1982, Butler 1984). Further, the number of nymphal instars is not constant for a particular species, but may vary with sex and environmental conditions, such as temperature and nutrition, during development (Brittain 1990). Although voltinism has been determined for many species, the number of instars has been published for only a few. For example, the number of instars for *Stenonema canadense* Walker is between 40 and

45 (Ide 1935), *Ephemera simulans* Walker approximately 30 (Ide 1935), *Ameletus celer* McDunnough 21 (Benton and Pritchard 1988), and *S. modestum* (Banks) 14–15 in the overwintering brood (Kondratieff and Voshell 1980).

Although mayflies characteristically are heterogeneous in growth, morphological development, and instar number (Fink 1982), studies of growth and development often rely on body measurements. An early method, introduced by Ide (1935), was based on the change in segmentation of the caudal filaments. The number of instars that a fully grown nymph has passed through may be estimated by counting the number of segments of the caudal filaments. However, it is difficult to obtain specimens from the field with intact caudal filaments, particularly in a quantified manner. A commonly used metric for mayflies and many other insect taxa is that of head capsule width (e.g., Kondratieff and Voshell 1980), which after direct measurement, are categorized into size classes. The most commonly used methods for mayfly instar determination are rearing, with direct observation of instars, and the simple frequency method, in which instars are indirectly determined by plotting the number of individuals per size class (Fink 1984). Another popular method is the Janetschek method which requires the calculation of a moving average of each simple frequency size class. However, head capsule width, the simple frequency and Janetschek methods, as well as others including the Cassie method and Dyar's Law, have been suggested as unreliable (Fink 1984). In a study that examined the utility of six mensural characters of *Ephemera danica* Muller (Ephemeridae) for determining growth and voltinism, size classes were established based on head capsule width (Aguayo-Corraliza et al. 1991). However, the data were not used to approximate instar number. In that study, only wingpad length was shown to exhibit allometric growth; whereas, body, head, and leg lengths and widths exhibited isometric growth.

Among mid-temperate mayflies, univoltine life cycles are the most common (Brittain 1990), whereas tropical and subtropical populations can deviate from this pattern with shorter, aseasonal life cycles (e.g., Nolte et al. 1996). The duration of a life cycle depends in part on factors that influence growth and development in all life stages. Also, genetic constraints that limit rates of these processes may exist (Butler 1984). Although thermal regime can have a major influence on voltinism of aquatic insects, life history patterns are the result of a complex bioenergetic interaction between temperature and food abundance and quality (Anderson and Cummins 1979, Sweeney 1984).

The family Heptageniidae is widely distributed throughout the Holarctic region and comprises a diverse component of benthic communities in Oriental (Dudgeon 1996) and Palearctic streams. More specifically, heptageniid nymphs of the genus *Stenonema* frequently are the most abundant benthic insects in streams and rivers of eastern North America (Bednarik and McCafferty 1979). The elucidation of the complete life cycle and life histories of these mayflies and other aquatic insects in the stream community is fundamental for a complete understanding of community dynamics (Richardson and Tarter 1976). This research was conducted to determine if using a suite of nymphal morphological characters with multivariate statistical analyses would provide greater resolution than other commonly used techniques in estimating the number of instars for a given mayfly species. Further, to examine voltinism, head capsule widths were taken and size-frequencies were calculated for four lotic mayfly species.

Materials and Methods

The site selected for life history studies was the Meramec River at the University of Missouri Hugo Wurdack Research Farm in

Crawford County, Missouri. At this locality, the Meramec River is a 5th order stream located in the Meramec River Basin, which is in the Ozark Plateau physiographic region. The study area is within a cleared/grazed land use area with a narrow, natural riparian zone. Riffle habitats were quantitatively sampled with a Surber sampler, which has a base area of 30.5 × 30.5 cm (1 ft^2) and mesh openings of 1 mm. The sediment within the frame was disturbed to a depth of approximately 6 cm with a hand rake for approximately 1 min. Benthic invertebrates collected into the net of the sampler were transferred into bottles containing 80% ethyl alcohol and transported to the laboratory. The sampling regime for 1992–93 consisted of weekly collections of 40 samples from mid-May through late September, and monthly collections for the remainder of the sampling year, for a total of 28 sampling dates.

Instar determination of *Stenonema mediopunctatum* (McDunnough).—Of the mayfly nymphs collected, *S. mediopunctatum* occurred consistently and in large numbers, making it a candidate taxon for analysis of body measurements and instar determination. Nymphs of *S. mediopunctatum* from representative subsamples of 13 of the 28 collecting dates, from May through November 1992, were measured (mm) using an ocular micrometer. Measurements consisted of head length and width, body width, and lengths of the profemur, protibia, mesofemur, mesotibia, metafemur, and metatibia. Head capsule was measured at the greatest width, which included the compound eyes. Body width also was measured at its greatest width, which was the pronotum. A total of 322 specimens was examined.

Cluster analyses were performed for head capsule width separately, and for the entire data set, which included all nine mensural characters. Hierarchical methods of classification, or cluster analyses, operate on a matrix of similarities among a set of units. This technique places variables that are highly correlated and similar to each other into groups and excludes from clusters those variables that are unlike. With the average linkage method (UPGMA), the distance between two clusters is the average distance between pairs of observations, one in each cluster. This analytical technique is a commonly used tool in morphometric research (e.g., Strauss 1992, Wool and Manheim 1992).

Because shape change accounts for significant variation among instars of insects undergoing allometric development, the data were ln-transformed and all body measurements again were clustered. Only a single dimension can be examined with linear measurements; therefore, the ln-transformed values were used to provide a mathematical approximation of shape by calculating two-dimensional variables [ln A + ln B = ln (A * B)].

After cluster analysis had grouped the individuals, first-level (most similar) groupings were assumed to represent instars and were numbered. These instar numbers were then assigned to all individuals in the original database. Discriminant function analysis (DFA) simultaneously maximizes intergroup differences and minimizes intragroup variation among individuals by altering the linear combination of variables on each of a number of orthogonal axes. DFA then was used to determine the degree of overlap among the clustered groups (instars), giving an indication of the range of variation within and among instar groupings. The subsequent classification phase of DFA then assigns each specimen to an instar based on the linear combination of variables from each discriminant function axis. Percent of correct assignments was used as a separate measure of morphometric distinction among instars. More specifically, percent correct classification was used to determine the accuracy of instar assignments. All statistical analyses were conducted using SPSS, version 4.0 (SPSS Inc., Chicago, IL).

Voltinism determination of lotic mayflies.—The four species chosen for analysis

of voltinism were those with nymphs that were collected throughout the year: *S. mediopunctatum* (Heptageniidae), *Tricorythodes curvatus* Allen (Leptohyphidae), *Caenis hilaris* (Say), and *C. latipennis* Banks (Caenidae). A black light was used to collect adult mayflies, and was positioned near the stream 12 h prior to each collection period. Using an ocular micrometer, nymphal head capsule measurements were tabulated for approximately 600–700 specimens of each of the four species from 17 of the 28 collecting dates (May 1992 through April 1993). The number of specimens collected and measured per month for *S. mediopunctatum* ranged from 15 to 54, whereas *T. curvatus* ranged from 4 to 50, *C. hilaris* from 3 to 50, and *C. latipennis* from 6 to 50. Size-frequency histograms then were constructed to determine voltinism.

Results

Instar determination of *Stenonema mediopunctatum*.—Using cluster analysis, raw data of head capsule width measurements clustered into five distinct groups at a small dissimilarity distance (Fig. 1A). The DFA classification rate was 89.6% using this approach. When raw data of all mensural characters were clustered, the data again exhibited five distinct groups (Fig. 1B), however the DFA classification rate improved to 95.6%. Finally, ln-transformed data for all mensural characters clustered into nine groups (Fig. 1C), and still maintained a high level of DFA classification (95.3%), indicating very distinct groupings.

Voltinism determination of lotic mayflies.—*Stenonema mediopunctatum* showed mainly incosistent size-frequency distributions throughout the year, although some patterns can be observed (Fig. 2A). The largest head capsule width measurements occurred in May and April for 1992 and 1993, respectively, although the frequencies of these measurements were low. Numbers remained high throughout the growing season for this species, and adults emerged during June, July, and August.

Tricorythodes curvatus exhibited very small changes in size-frequency distributions throughout the year (Fig. 2B). From May through September, head capsule widths were as high as 1 mm; however, from October through April, the population was represented primarily by higher frequencies of smaller individuals. Adults of this species emerged during June, July, August, and September, and a second cohort can be observed in September.

Caenis hilaris was the least abundant of the four species examined, and no specimens were collected during December, January, February, or March (Fig. 2C). Peak abundance and the largest specimens occurred during early summer months (i.e., late April, May, June). *Caenis latipennis* exhibited a pattern similar to that of *C. hilaris*, with the largest sized individuals occurring in April and May (Fig. 2D). Adult emergence of both species of *Caenis* occurred during June through September.

Discussion

Analysis of mensural characters of *S. mediopunctatum* nymphs revealed that at least nine instars were present in the samples from the Meramec River during the study period. Because a single outlier existed in each analysis, representing an instar markedly dissimilar from the others, it is likely that the morphometric distribution does not represent a contiguous succession of instars. Using a suite of ln-transformed body measurements provided increased resolution over using non-transformed data and increased resolution and precision over using head capsule widths alone. Cluster analysis for head capsule widths resulted in five instars and the lowest classification rate (89.6%) of the three methods evaluated. Thus, a relatively high degree of overlap (11.4%) existed among groups (instars) when based on only a single variable. When a suite of nine mensural variables was used, the number of instars remained unchanged, although classification accuracy increased dramatically to 95.6%. Thus, the number of

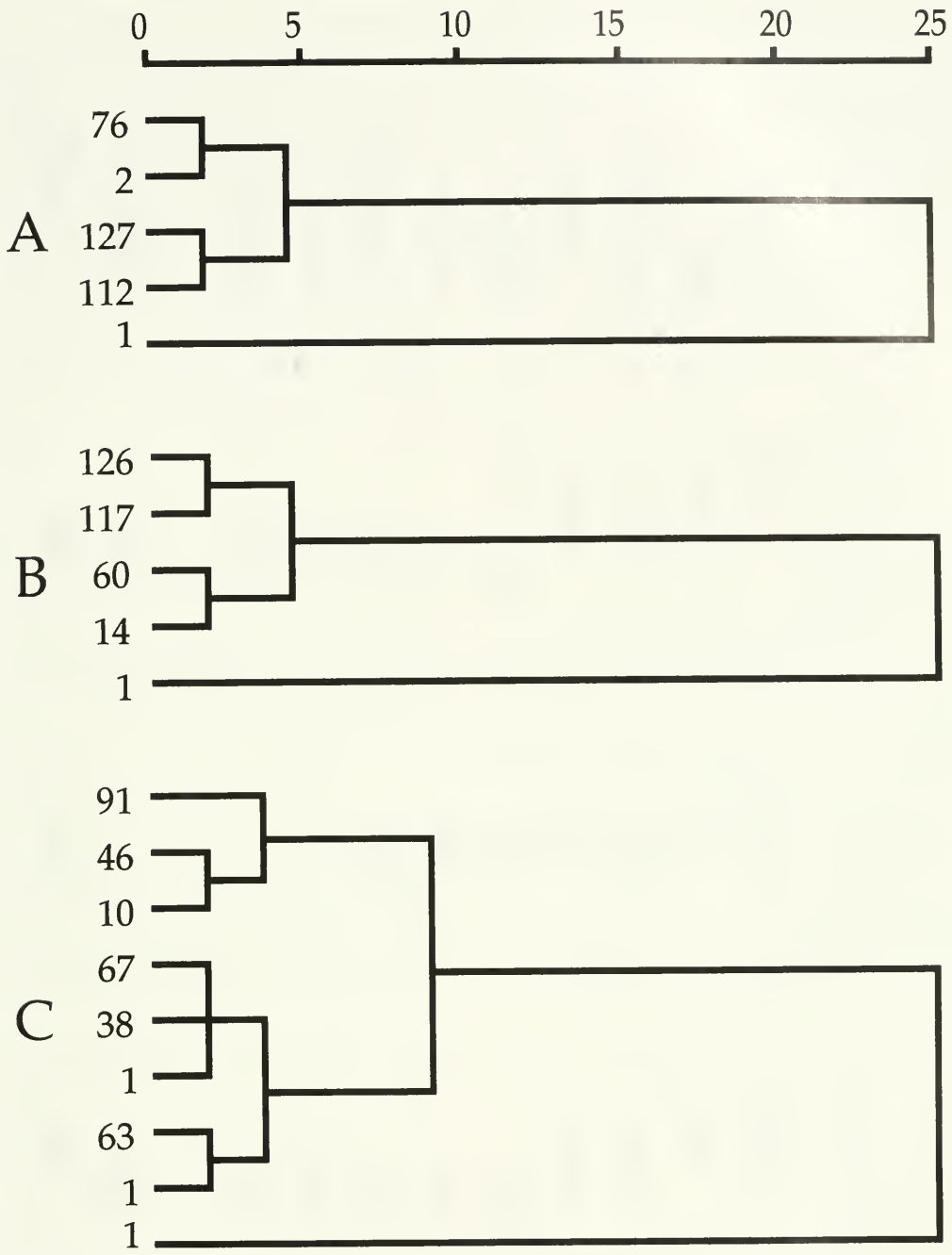

Fig. 1. Dendrogram of cluster analysis of *Stenonema mediopunctatum* nymphs based on measurements of (A) head capsule widths, (B) raw data of nine body characters, and (C) ln-transformed data of nine body characters. Numbers on the left of each dendrogram indicate the number of individuals within a given cluster.

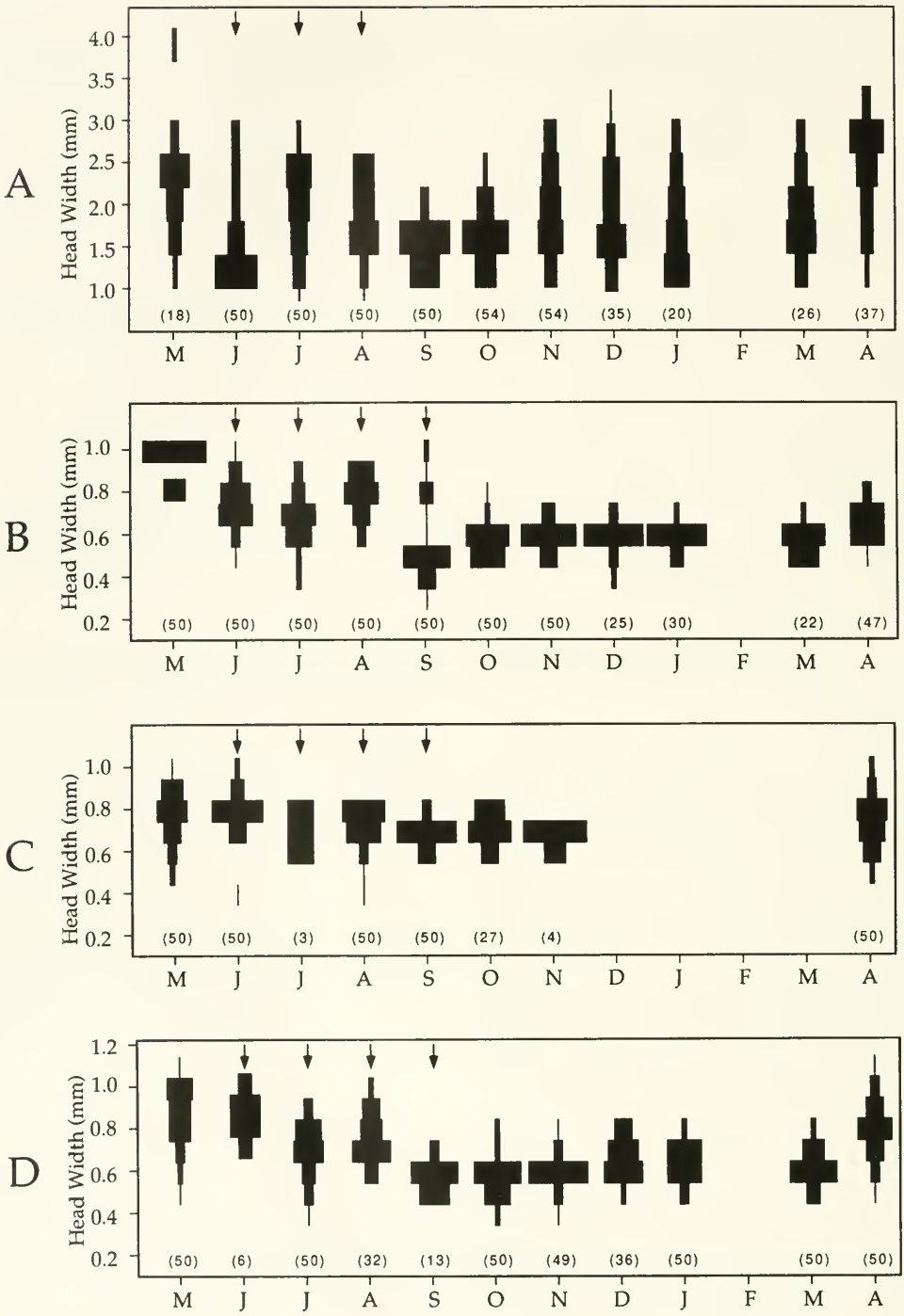

Fig. 2. Percent of individuals in each head capsule size class within each sample of four species of Ephemeroptera collected from the Meramec River from March 1992 through April 1993. A) *Stenonema mediopunctatum*, B) *Tricorythodes curvatus*, C) *Caenis hilaris*, D) *Caenis latipennis*. Arrows indicate adult presence in black light samples, numbers in parentheses indicate the number of immatures measured.

misclassifications was approximately halved while maintaning the same level of grouping resolution. The use of ln-transformed variables provided dramatically increased discrimination among groups, and cluster analysis identified nine groups. All characters were highly correlated with DFA axis 1 and accounted for >95% of the variation for both raw data and ln-transformed data. Thus, all characters measured were important in discriminating among instars. Although the resolving power of the ln-transformed data set nearly doubled the number of discernible groups, classification accuracy remained high at 95.3% (i.e., 4.7% of cases were assigned to the incorrect group). Clearly, the possibility exists that additional instars exist that were not discerned. Nonetheless, by using a suite of ln-transformed variables, this method of instar determination represents a significant improvement over the commonly used head capsule width analysis because both resolving power and precision are substantially increased.

Insects with a small number of distinct instars may have greater inter-instar variance in size than intra-instar variance, which allows for the number of instars to be effectively discerned using techniques such as the multivariate analysis of body measurement presented here. For example, Sites (1991), using such methods, confirmed that *Pelocoris poeyi* (Guerin Meneville) (Heteroptera: Naucoridae) has five nymphal instars. In mayflies, overall increase in size of the nymph occurs at each molt as well as a differential growth rate of body parts (allometric growth); therefore, one function of molting is to change morphological structure (Ide 1935). Although the method discussed here was shown to improve our ability to discriminate among instars from a field population, laboratory rearing of mayflies would provide the most accurate data, although environmental influences on body size and shape and instar number would not be realized.

Population studies of species of *Stenonema* have revealed mainly univoltine winter cycles, which are characterized by a single generation overwintering in the nymphal stage (Clifford 1982). The pattern observed during this research for *S. mediopunctatum* approximates this pattern, with overwintering nymphs, continued growth throughout spring, and emergence in early summer. The wide variation in frequency values and inconsistent patterns most likely indicate a large number of nymphal instars present in the stream at a given time.

Temperate populations of *Tricorythodes* generally have been characterized as multivoltine (Clifford 1982). Although some temporal size shifts were observed during this study, a pattern was not clear. Because multivoltine life history patterns typically would be evidenced by a wide range of sizes of individuals throughout the year, *T. curvatus* apparently also is multivoltine in this region.

Life histories of many *Caenis* populations have been reported to be quite flexible (Clifford 1982). Nearly half of the *Caenis* species for which life histories have been documented are univoltine winter and half are bivoltine winter-summer, with an overwintering generation in the nymphal stage and one summer generation (Clifford 1982). For both *Caenis* species examined here, the largest individuals occurred from late April through mid-June, with a summer emergence period over four months (June–September). Therefore, it appears that both *C. hilaris* and *C. latipennis* have a univoltine life history with an overwintering nymphal stage. Black light collections of adults of these species also support univoltinism.

Geographic variation in voltinism due to thermal or nutritional regimes commonly has been reported (Sweeney 1984); however, even within populations, variability in life cycle duration can exist (Butler 1984). Therefore, because of the potential for environmentally induced variation that exists for the majority of aquatic insects (Wallace

and Merritt 1980), life history attributes, such as instar number and voltinism, should not necessarily be considered species specific traits, but should be examined on a regional basis for each population. Larger sample sizes may have improved resolution in the size-frequency graphs, although a high degree of variation is inherent, and should be expected, in mayfly populations.

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A REVISION OF *THAUMASIOCHAETA* STEIN AND ALLIED GENERA (DIPTERA: MUSCIDAE: COENOSIINAE: LIMNOPHORINI)

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Abstract.—*Thaumasiochaeta, Mesochaeta, Teleutochaeta* and *Rhyncholimnophora* were described by Stein, respectively with one, two, one and three species. Few references to these taxa have been made in the literature since the original descriptions. Examination of the types showed that all the species could be considered as congeneric and are treated so in this paper. The characters originally used to distinguish them are mainly those of the male sex. *Thaumasiochaeta* is considered to be the senior synonym. The following **new combinations** are proposed: *T. compressitarsis, T. haustellata, T. incaica, T. longipalpis, T. nigriceps* and *T. variegata*. The genus and all the species are redescribed, with illustrations. A key to species is provided.

Resumo.—*Thaumasiochaeta, Mesochaeta, Teleutochaeta* e *Rhyncholimnophora* foram descritos por Stein, respectivamente para uma, duas, e três espécies. Desde a descrição original, poucas referências a estes taxa foram feitas na literatura. O exame dos tipos mostrou que todas as espécies podem ser consideradas como congenéricas e são tratadas como tal neste artigo. Os caracteres originalmente utilizados para distinguí-las são, principalmente, do sexo masculino. *Thaumasiochaeta* é considerado como sinônimo senior. As seguintes **novas combinações** são propostas: *T. compressitarsis, T. haustellata, T. incaica, T. longipalpis, T. nigriceps* e *T. variegata*. O gênero e todas as espécies são redescritas, com ilustrações. Uma chave para identificação das espécies é fornecida.

Key Words: *Thaumasiochaeta*, Diptera, Muscidae

A large number of new Diptera species were described by Stein (1911) based on material collected by Schnuse in South America (Chile, Peru, and Bolivia), including specimens from 4,000 m. altitude. According to Stein (1911) some flies, especially the ones from higher altitudes, were of extraordinary beauty, with remarkable structures and bristles on some parts of the body. Stein (1911) also stated that few new genera were described, as he preferred to assign the new species to known genera (e.g., the large number of species described in *Limnophora* and *Coenosia*). The description of new genera was restricted to some material collected around Lake Titicaca (country), in which males sex had some striking modifications. Among these new genera were: *Thaumasiochaeta* (*T. pilitarsis*), *Mesochaeta* (*M. variegata* and *M. incaica*), *Teleutochaeta* (*T. nigriceps*) and *Rhyncholimnophora* (*R. compressitarsis, R. haustellata* and *R. longipalpis*). The original descriptions of all four genera mentioned the morphological similarity among them, and the characters used to diagnose them were mainly confined to the male sex. Since the original descriptions these taxa

have been listed in catalogues but otherwise have received only incidental mention. No further species have been described.

Thaumasiochaeta was diagnosed by the presence in the male of a filiform appendix to the arista that ends in a triangular expansion, and *Mesochaeta* by the presence in the male of a very long bristle on apical third of dorsal surface of fore tibia, ending in a triangular expansion. The other two genera, *Teleutochaeta* and *Rhyncholimnophora*, were compared with these genera as they were very similar to them. *Teleutochaeta* was distinguished by the narrow orbits at the base of the antenna, the labrum conspicuously projecting, the modified bristle on the fore tibia placed near apex, and the absence of wing-clouds. *Rhyncholimnophora* was differentiated from *Thaumasiochaeta* by having a simple arista and from the other two by the absence of the modified bristle on the dorsal surface of the fore tibia.

Subsequent authors treated these taxa differently. Séguy (1937) considered *Rhyncholimnophora* and *Thaumasiochaeta* as good genera, differing from one another by the extent of the epistomal projection. *Mesochaeta* and *Teleuchaeta* were considered synonyms of *Thaumasiochaeta*. Pont (1972) considered *Thaumasiochaeta* and *Rhyncholimnophora* to be good genera, and *Mesochaeta* a synonym of *Teleutochaeta*.

The most recent catalogue of Neotropical Muscidae (Carvalho et al. 1993) followed Pont (1972), but no types or other material were examined. The genus was assigned to the Coenosiinae, tribe Limnophorini.

The four genera differ from all other Limnophorini by the epistomal projection, the presence of setulae on the anepimeron, meron (below posterior spiracle) and sides of scutellum, the wings with strong spines along costal margin and hind tibia with a median and a supramedian bristle on posterodorsal surface, and also by the black color and the extra hairs and setulae, which are adaptations commonly found among high-altitude Muscidae. This set of characters is not found in any other muscid.

This review was prompted by examination of the type material deposited in the Staatliches Museum für Tierkunde (SMT), Dresden, Germany, and in the Zoologisches Museum der Humboldt-Universität (ZMHU), Berlin, Germany. All the species are now considered to belong to the same genus, *Thaumasiochaeta,* which is chosen as the senior synonym. A revised generic description is given. The type-species *Thaumasiochaeta pilitarsis* is fully redescribed and the other species are compared with it. Several new combinations are proposed. Bibliographic references for each species are given by Carvalho et al. (1993), and only the reference to each original description is given here.

Thaumasiochaeta Stein

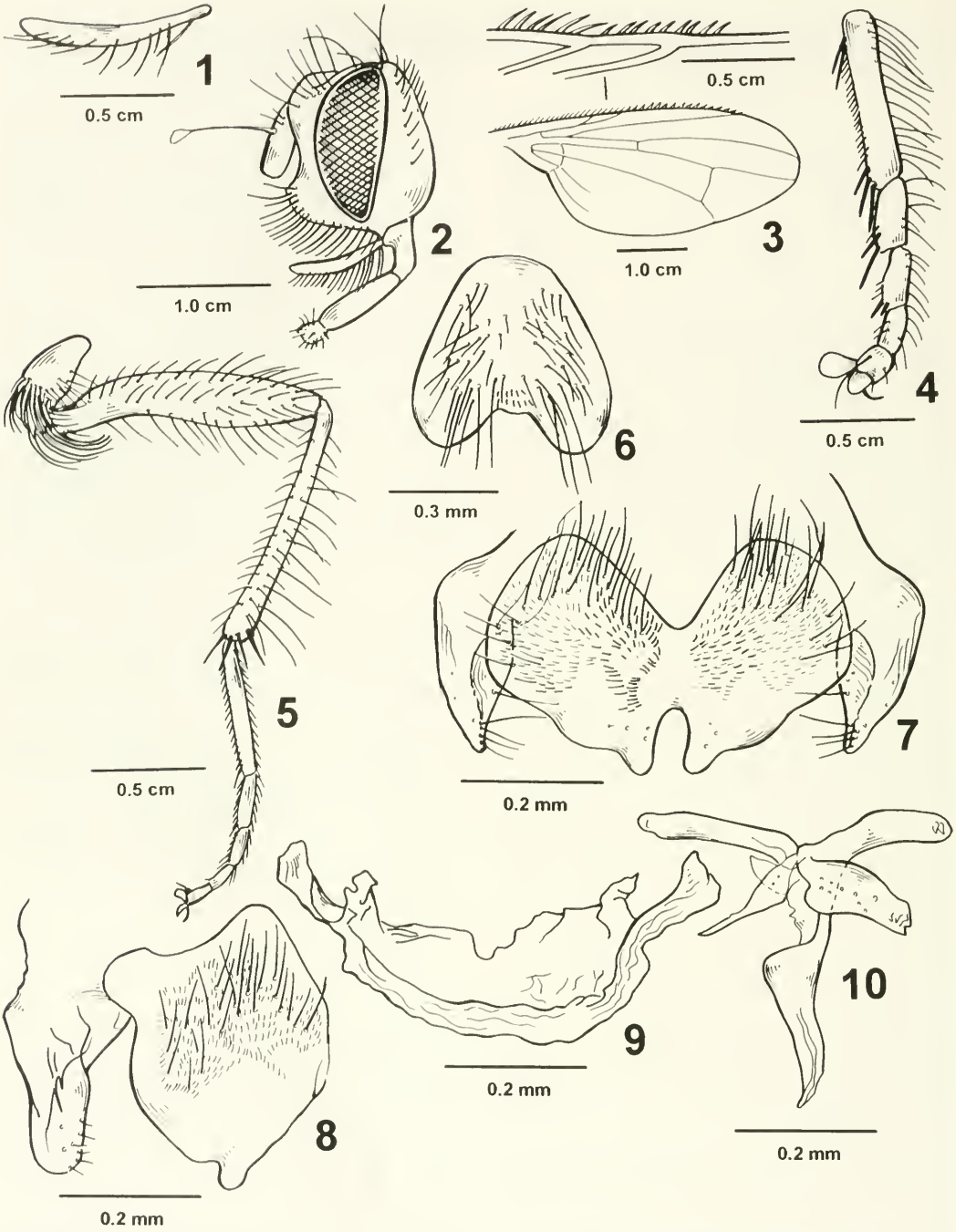
Thaumasiochaeta Stein 1911: 137.
Type species: *Thaumasiochaeta pilitarsis* Stein, by monotypy.

Mesochaeta Stein 1911: 139 [preocc.].
Type species: *Mesochaeta variegata* Stein, desig by Séguy 1937.

Teleutochaeta Stein 1911: 141.
Type species: *Teleutochaeta nigriceps* Stein, by monotypy.

Rhyncholimnophora Stein 1911: 142. **New synonymy**.
Type species: *Rhyncholimnophora compressitarsis* Stein, desig. by Séguy 1937.

Diagnosis.—Male dichoptic; frons very wide, about ½ of head width; epistomal projection variable: not far projecting in *T. variegata* (Figs. 15, 24), *T. incaica* and *T. pilitarsis* (Fig. 2), and strongly projecting in *T. nigriceps* (Figs. 29, 36) and *T. longipalpis* (Fig. 51). Ocellar triangle with a pair of long bristles near anterior ocelli and about 6 other finer and shorter bristles (only one pair in *T. haustellata* and *T. longipalpis*). Antenna with flagellomere large, arista bare, enlarged at base; palpus long, broad and flattened (Fig. 1). Dorsocentral bristles 2:3; pre-alar bristle absent; scutellum with



Figs. 1–10. *Thaumasiochaeta pilitarsis*. 1, Male palpus. 2, Male head (profile). 3, Male wing. 4, Male hind tarsus, anterior view. 5, Male hind leg, anterior view. 6, Male sternite 5. 7, Cercal plate and surstyli (dorsal view). 8, Cercal plate and surstyli (lateral view). 9, Hypandrium. 10, Aedeagus (lateral view).

setulae laterally; prostemum setulose; proepisternals 2, proepimerals 2; postpronotal lobe with 2 long bristles; notopleuron with 2 long bristles, the anterior a little longer than the posterior; with setulae in addition to the bristles; katepisternum with long and fine cilia on disc; katepisternals 1:1 (1:2 in *T. longipalpis*), the upper posterior one about twice as long as the other; lower calypter about 1.5 the length of upper one; anepimeron setulose, with long and fine setulae; meron with setulae below posterior spiracle; wings with strong spines along costal margim (Fig. 3); stem vein with ventral surface bare (setulose in *T. longipalpis*); R_1 on dorsal surface with cilia in apical fourth (along entire length in *T. longipalpis*); base of R_{2+3} and R_{4+5} with setulae on both surfaces. Sternite I setulose. Proboscis with haustellum totally sclerotized, shining (Fig. 11). Hind tibia on posterodorsal, anterodorsal and dorsal surfaces with a preapical bristle. Ovipositor with microtrichia on membrane of segment 7 and spicules on membrane of segment 8 (Figs. 12–13).

Geographical distribution.—Neotropical, the high Andean Cordillera of Peru and Bolivia.

Discussion.—The genus can be distinguished from the other Limnophorini by the epistomal projection and by the presence of setulae on the anepimeron and meron; setulae at sides of scutellum; hind tibia with long median and supramedian bristles on posterodorsal surface. The black color and the presence of numerous additional hairs and setulae are adaptations for higher altitudes.

Key to Adults

Males are easy to separate as they have many unique characters such the modifications of the arista, leg chaetotaxy and mid femur curvature. On the other hand, females are very similar and difficult to distinguish.

1. Katepisternals 1:1; R_1 on dorsal surface setulose at apex; R_{4+5} with setulae only at base . . 2
– Katepisternals 1:2; R_1 on dorsal surface setulose along entire length; R_{4+5} with cilia extending as far as r-m . . . . . *T. longipalpis* (Stein)
2. Ocellar triangle with six or more bristles in addition to the ocellar pair; male with or without a depression on basal third of hind femur . . . 3
– Ocellar triangle with no bristles, apart from the single pair; male without a depression on basal third of hind femur . . . . . *T. haustellata* (Stein)
3. Epistoma not strongly projecting (Figs. 2, 15, 40); lower calypter with margin whitish or brown; male without a preapical bristle with a triangular apex on dorsal surface of fore tibia 4
– Epistoma strongly projecting (Figs. 29, 36); lower calypter with margin brown; male with a preapical bristle with triangular apex on dorsal surface of fore tibia . . . . *T. nigriceps* (Stein)
4. Lower calypter with whitish margin; male with arista not triangular at apex 5
– Lower calypter with brown margin; male with arista triangular at apex . . . . . *T. pilitarsis* (Stein)
5. Wings clouded as in Fig. 14; male with fore tibia on dorsal surface with a median bristle with triangular apex . . . . . *T. variegata* (Stein)
– Wings clouded or hyaline; male without a very long median bristle with triangular apex on dorsal surface of fore tibia 6
6. Wings hyaline . . . . . *T. compressitarsis* (Stein)
– Wings clouded as in Fig. 28 . . *T. incaica* (Stein)

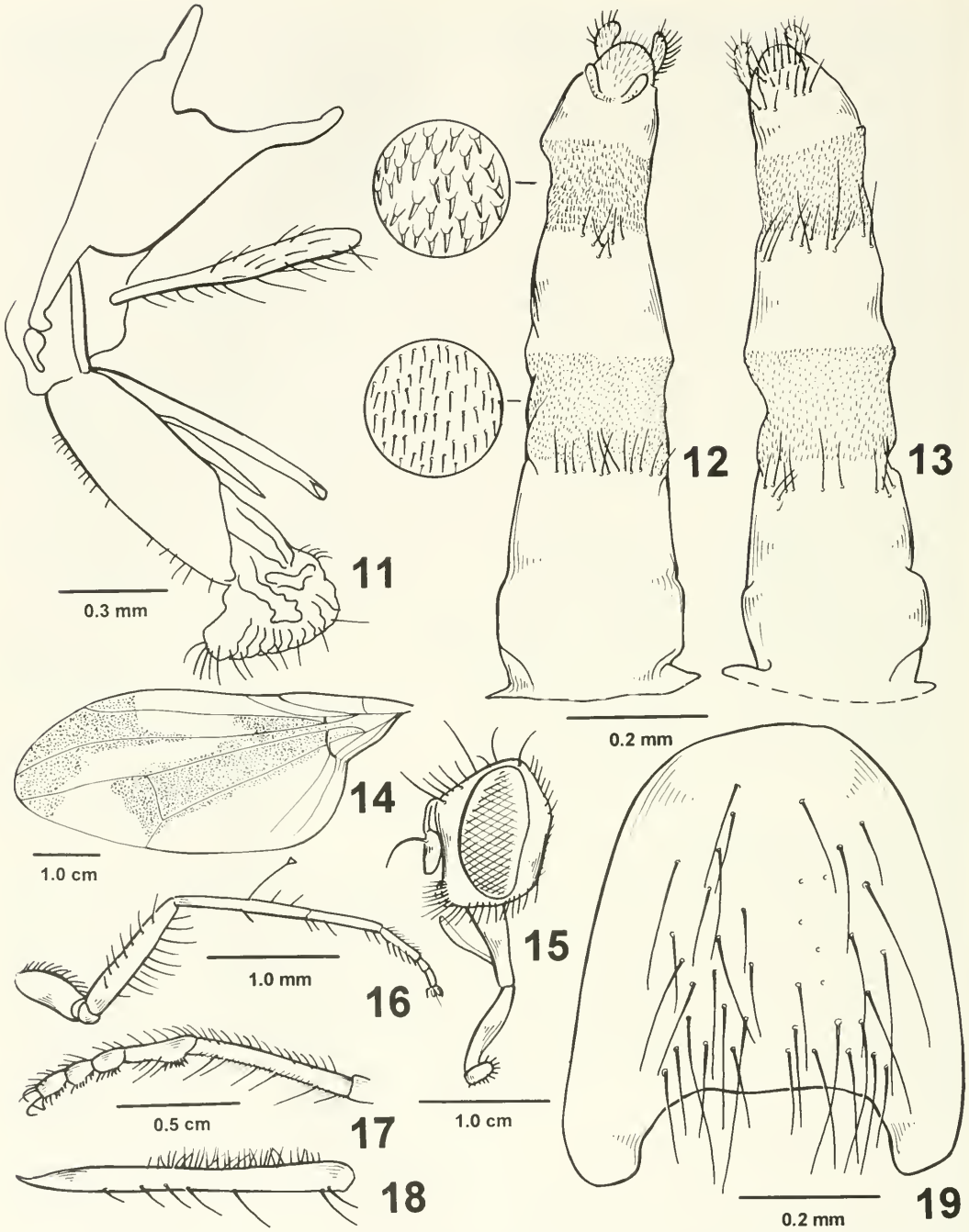
Thaumasiochaeta pilitarsis Stein (Figs. 1–13)

Thaumasiochaeta pilitarsis Stein 1911: 138.

Diagnosis.—Lower calypter with brown margin; wing yellowish. Male with arista triangular at apex (Fig. 2). Fore tarsomere I on anterodorsal, dorsal and posterodorsal surfaces with a complete row of long bristles; ventral surface with strong bristles at base and apex and some short bristles on middle. Fore tarsomere II on ventral surface with 3–4 long and strong apical bristles, the most apical one the strongest. Fore tarsomere III on ventral surface with 2–3 strong apical bristles (Fig. 4). Hind leg (Fig. 5) with coxa and trochanter with a tuft of bristles; femur on ventral surface curved in basal half.

Male.—Length: body: 5.0–5.5 mm; wing: 4.8–5.0 mm.

Color: Frons and fronto-orbital plates dark brown, strongly silvery pollinose on basal third near lunule. Face, parafacial and



Figs. 11–19. 11–13. *Thaumasiochaeta pilitarsis*. 11, Female proboscis. 12, Ovipositor (dorsal view). 13, Ovipositor (ventral view). 14–19. *T. variegata*. 14, Male wing. 15, Male head (profile). 16, Male fore leg, anterior view. 17, Male fore tarsus, anterior view. 18, Male hind tibia, anterior view 19, Male sternite 5.

gena brown, parafacial also strongly silvery pollinose. Antenna dark brown. Arista and palpus brown. Calypter whitish, lower one with brown margin. Wing yellowish. Haltere yellow at base and brown on apical two-thirds. Legs dark brown. Abdomen bluish-grey pollinose dorsally from certain angles.

Head: Eyes bare; at level of anterior ocellus separated by 0.38–0.40 of head width. Inner and outer vertical bristles long, the latter one directed outwards. Frontal row with 6–7 pairs of long bristles, the upper two directed outwards. Antenna with flagellum 1.3–1.5 times as long as pedicel.

Thorax: Acrostichal hairs distinct, irregular throughout. Presuturals 1; supraalar 1; post-supraalar 2. Scutellum with a pair of lateral bristles at middle and an apical pair, both long. Fore femur on anterior, dorsal, anterodorsal, ventral and anteroventral surfaces with complete rows of bristles. Fore tibia on anterodorsal surface with a row of bristles on apical half; dorsal and posterodorsal surfaces with complete rows of long and fine bristles; dorsal, posterodorsal and posterior surfaces with an apical bristle. Fore tarsomere I on anterodorsal, dorsal and posterodorsal surfaces with complete rows of long bristles, ventral surface with strong bristles at base and apex and some short bristles at middle; tarsomere II on ventral surface with 3–4 long and strong apical bristles, the most apical one the strongest; tarsomere III on ventral surface with 2–3 strong apical bristles (Fig. 4). Mid coxa on anterior surface with strong and long bristles. Mid femur on anterior, anterodorsal and anteroventral surfaces with long bristles. Mid tibia on all surface with long and fine bristles; anterodorsal surface with 3–4 bristles on middle third, anteroventral surface with 2–3 bristles on middle third; dorsal surface with a preapical bristle; posterior, posterodorsal, anterodorsal and anterior surfaces with an apical bristle. Mid tarsomere I on ventral surface with a row of bristles, the apical one the strongest. Hind leg (Fig. 5) with coxa and trochanter with a tuft of bristles. Hind femur on ventral surface with curved in basal half; anterior, anterodorsal, anteroventral, dorsal and ventral surfaces with long bristles. Hind tibia on anteroventral and anterodorsal surfaces with long bristles, dorsal surface with a preapical bristle; anterodorsal, anteroventral and ventral surfaces with an apical bristle.

Abdomen: Tergite 5 with two discal rows of bristles and one marginal. Sternite 5 with lateral bristles; no bristles on longitudinal middle third longitudinally (Fig. 6).

Terminalia: Cercal plate wider than long (Figs. 7, 8); hypandrium large (Fig. 9); distiphallus long, enlarged at base (Fig. 10).

Female.—Length: body: 6.0–6.3 mm; wing: 5.5–6.0 mm.

Differs from male as follows: frons, fronto-orbital plates, parafacial and gena lighter, with weak pollinosity. Abdomen less pollinose. Arista with apex not modified. Leg chaetotaxy less numerous, tarsal bristles fine. Mid tibia on anteroventral surface with 3–4 bristles in apical half, anterodorsal surface with a row of bristles, posterior surface with a row of bristles on apical 2/3. Tuft on hind coxa and trochanter weak, with few bristles. Hind femur not modified.

Terminalia: Cerci longer than epiproct, both with microtrichia. Hypoproct without microtrichia (Figs. 12, 13).

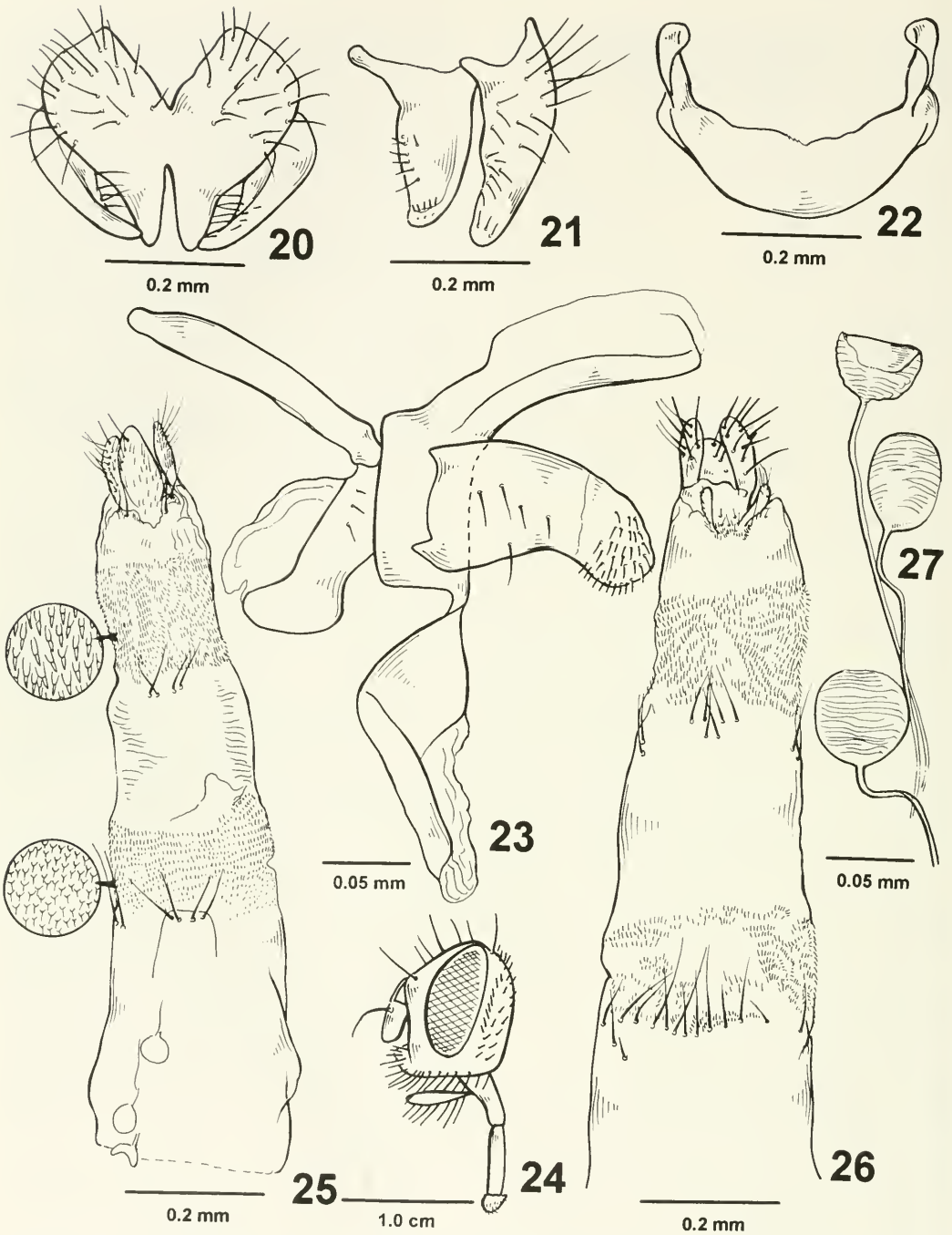
Material examined.—Stein (1911) described this species from 6 pairs from Peru (Puno) and Bolivia (Tiahuanaco). Four ♂ and 5 ♀ syntypes have been studied as follows: PERU, Puno, 17.xi.02 (Schnuse), 3 ♂ and 1 ♀ (SMT); 20.xi.02 1 ♀ (SMT); 21.xi.02 1 ♀, 1 ♂ (SMT); BOLIVIA, Tiahuanaco, 30.v.03 1 ♀ (SMT); 19.xi. 02, 1 ♀ (ZMHU).

Thaumasiochaeta variegata (Stein), **new combination**

(Figs. 14–27)

Teleutochaeta variegata Stein 1911: 139.

Diagnosis.—Both calypters whitish; wing clouded (Fig. 14). Fore tibia on anteroventral surface with a short median



Figs. 20–27. *Thaumasiochaeta variegata*. 20, Cercal plate and surstyli (dorsal view). 21, Cercal plate and surstyli (lateral view). 22, Hypandrium. 23, Aedeagus (lateral view). 24, Female head (profile). 25, Ovipositor (dorsal view). 26, Ovipositor (ventral view). 27, Spermatheca.

bristle; dorsal surface with a median bristle with triangular apex; anterodorsal surface with 2–3 bristles on apical third. Fore tarsomere I on ventral surface with a spine at base and with about 5 bristles; tarsomeres II–V on ventral surface with a tuft of short bristles at middle followed by long bristles (Fig. 17). Hind femur not curved in basal third.

Differs from *T. pilitarsis* as follows:

Male.—Length: body: 4.0–4.2 mm; wing: 3.0–3.3 mm.

Color: Parafacial and gena densely golden pollinose. Haltere with stalk yellow and knob brown. Both calypters whitish. Wing clouded, as in Fig. 14.

Head (Fig. 15): Eyes at level of anterior ocellus separated by 0.45–0.48 of head width. Apex of arista not modified.

Thorax: Fore leg as in Fig. 16. Fore femur on anteroventral and anterodorsal surfaces with complete rows of bristles. Fore tibia on anteroventral surface with a short median bristle; dorsal surface with a median bristle with triangular apex; anterodorsal surface with 2–3 bristles on apical third. Fore tarsomere I on ventral surface with a spine at base and about 5 bristles; tarsomeres II–V on ventral surface with a tuft of short bristles at middle followed by long bristles (Fig. 17). Mid femur on ventral surface with fine bristles on middle third. Mid tibia on anterodorsal surface with 3–6 bristles on middle third; posterodorsal surface with 2–4 bristles inserted on middle third and a preapical bristle; dorsal surface with a long bristle on apical third; posterior, anteroventral, ventral, posteroventral and posterior surfaces with a preapical bristle. Mid tarsomeres not modified as on fore leg. Hind femur not curved in basal third; posterodorsal and posteroventral surfaces with 2–3 bristles in apical third. Hind tibia (Fig. 18) on anterior to anterodorsal surfaces with 4–5 bristles; anterodorsal and posterodorsal surfaces with a preapical bristle; ventral surface with short cilia on approximately basal two-thirds. Hind tarsi as on mid leg.

Abdomen: Lateral bristles on all tergites. Sternite 5 longer than wide (Fig. 19).

Terminalia: Cercal plate with anterior incision deep; surstyli broad (Figs. 20, 21). Hypandrium large (Fig. 22). Distiphallus larger at base, paramere with sensillae at apex (Fig. 23).

Female.—Length: body: 3.5–3.6 mm; wing: 3.0–3.2 mm.

Differs from male as follows: parafacial grey pollinose. All colors weaker than in male. Face more projecting (Fig. 24). Fore tibia on dorsal surface with a row of 4–5 bristles none with triangular apex; bristles on tarsi not modified. Hind tibia on anteroventral surface with 3 bristles on apical third.

Terminalia: Sternite 8 with two bristles on each half, cerci and epiproct with microtrichia (Figs. 20–21). 3 spermathecae, one round and two oval (Fig 22).

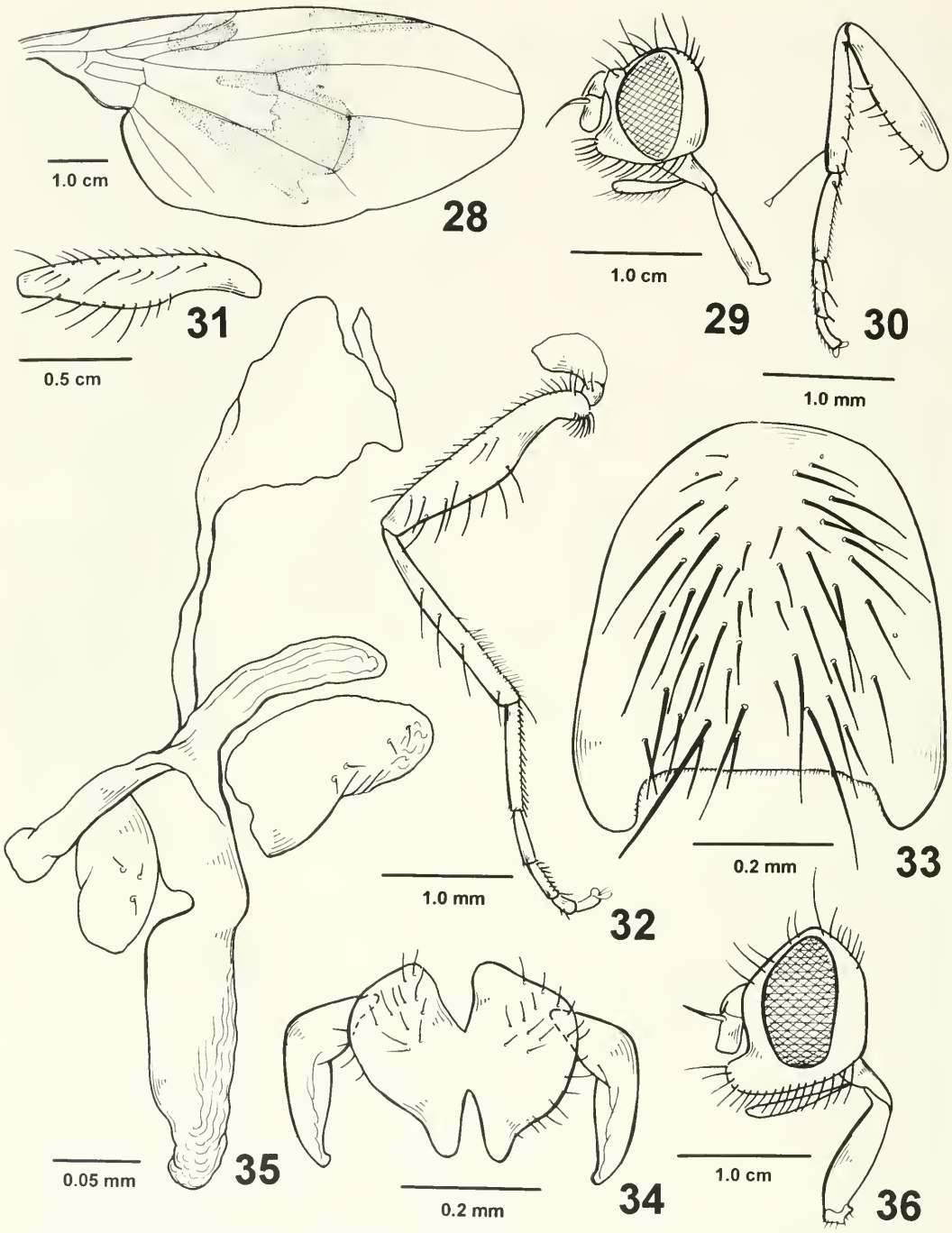
Material examined.—Stein (1911) described this species from 7 ♂ and 8 ♀ from Peru (Puno and Oroya) and Bolivia (Lake Titicaca). 5 ♂ and 3 ♀ syntypes have been studied as follows: PERU, Puno, 23.xi.02, 2 ♂ (SMT); 16.xi.02 3 ♂ and 1 ♀ (Schnuse) (SMT); Oroya, 21.i.04 1 ♀ (SMT). BOLIVIA, Titicaca, 30.v.03 (Schnuse) 1 ♀ (SMT).

Thaumasiochaeta incaica (Stein), **new combination**
(Figs. 28–29)

Teleutochaeta incaica Stein 1911: 140.

I have only examined one female, which is very similar to *T. variegata*, except for the wing color (Fig. 28). Stein (1911) separated the male of this species from male of *T. variegata* by: fore tarsus not modified; hind femur enlarged at middle of internal surface and with short ciliae.

Material examined.—The original series contained 2 ♂ and 5 ♀ from Bolivia (Titicaca). 1 ♀ syntype has been studied as follows: BOLIVIA, Titicaca, 11.vi.03 1 ♀ (ZMHU).



Figs. 28–36. 28, *Thaumasiochaeta incaica*. Female wing. 29–36. *T. nigriceps*. 29, Male head (profile). 30, Male fore leg, anterior view. 31, Male hind femur, anterior view. 32, Male hind leg, anterior view. 33, Male sternite 5, anterior view. 34, Cercal plate and surstyli (dorsal view). 35, Cercal plate and surstyli (lateral view). 35, Aedeagus (lateral view). 36, Female head (profile).

Thaumasiochaeta nigriceps (Stein), **new combination**

(Figs. 29–39)

Thaumasiochaeta nigriceps Stein 1911: 141.

Diagnosis.—Epistoma very projecting. Fore tibia on anteroventral surface with a median bristle; posterodorsal surface with 2 bristles on middle third; dorsal surface with a modified preapical bristle, triangular at apex. Hind tibia on anterodorsal surface with 3 bristles on middle third; posterior surface with 2 bristles on middle third; dorsal surface with a preapical bristle; ventral surface with an apical bristle; ventral surface with cilia on apical third.

Differs from *T. pilitarsis* as follows:

Male.—Length: body: 5.0–5.2 mm; wing: 5.0–5.2 mm.

Color: Parafacial a little golden from certain angles. Both calypters hyaline, border of lower one brown. Legs brown.

Head: Eyes at level of anterior ocellus separated by 0.36 of head width. Flagellomere 1.25 times as long as pedicel (Fig. 29).

Thorax: Fore leg (Fig. 30) with femur on anterodorsal surface with a complete row of bristles; anteroventral surface with a row of bristles on apical half; anterior surface with sparse bristles. Fore tibia on anteroventral surface with a median bristle; posterodorsal surface with 2 bristles on middle third; dorsal surface with a modified preapical bristle, triangular at apex; anterodorsal surface with a short preapical bristle inserted at the same level as the dorsal modified bristle; anterior surface with a supra-median bristle and a preapical one, both short and fine. Fore tarsi on ventral surface with short and strong bristles on tarsomeres I, II and III. Mid femur on anterior surface with a row of short bristles on apical two-thirds; anteroventral surface with a median bristle and a row of bristles on apical third; posteroventral surface with 2 preapical bristles. Mid tibia on anteroventral surface with a median and a submedian bristle, the latter one longer; posteroventral surface with a submedian bristle; dorsal surface with 3 bristles on middle third; posterior surface with 2 bristles on middle third; anterodorsal surface with a preapical bristle; anterodorsal, anteroventral, posterodorsal and ventral surfaces with an apical bristle, the latter the longest. Hind femur (Fig. 31) on anterodorsal surface with a depression on apical third; anteroventral surface with 2–3 apical bristles. Hind tibia on anterodorsal surface with 3 bristles on apical third, the median one short; posterior surface with 2 bristles on middle third; dorsal surface with a preapical bristle; anteroventral surface with an apical bristle; ventral surface with ciliae on apical third (Fig. 32)

Abdomen: Tergite 5 with a marginal and a discal row of bristles. Stemite 5 with posterior membrane straight (Fig. 33).

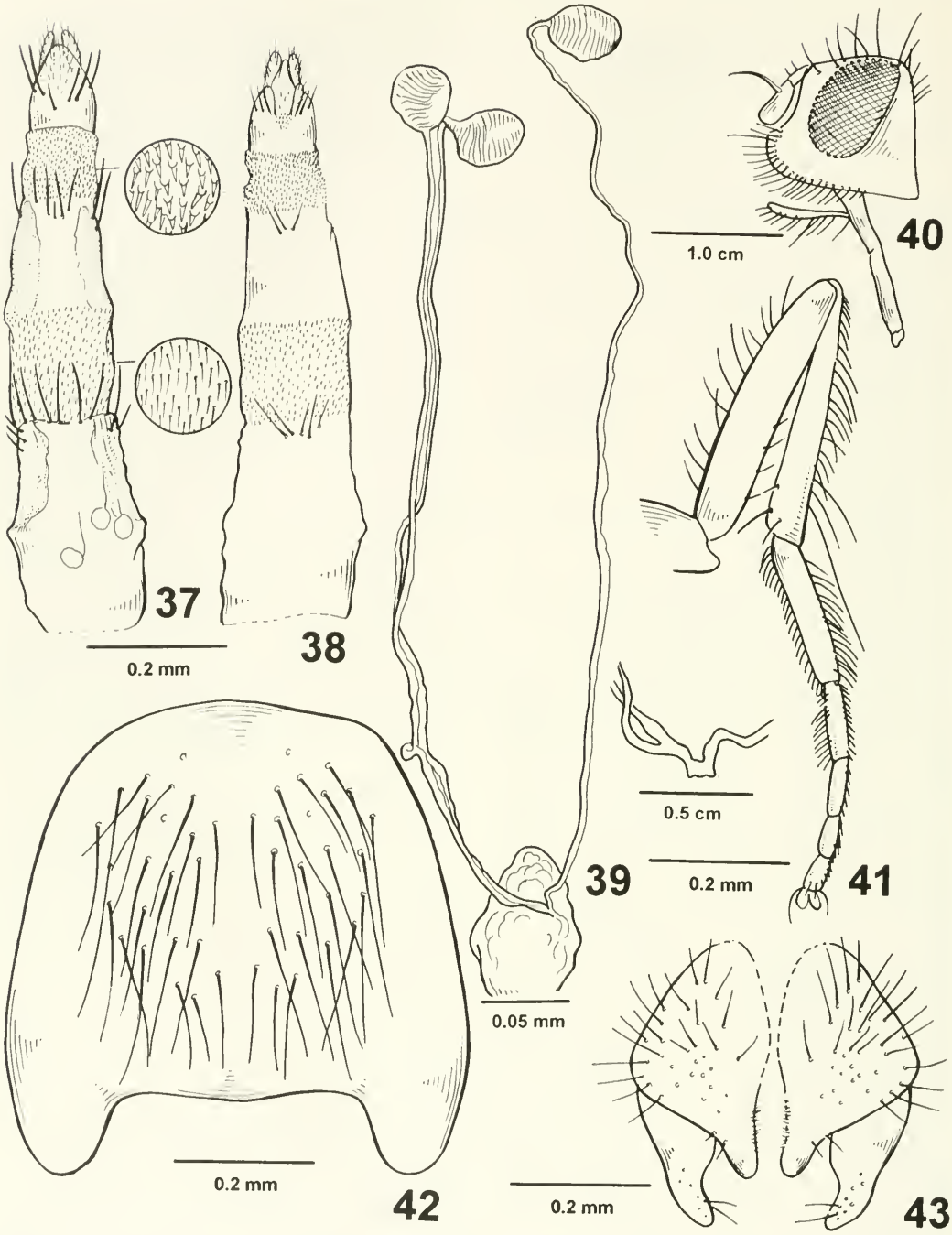
Terminalia: Cercal plate as long as broad, with a sharp incision on posterior side (Figs. 34–35); phallapodeme short, distiphallus long and cylindrical (Fig. 35).

Female.—Length: body: 4.8–5.1 mm; wing: 4.5–4.6 mm.

Differs from male as follows: parafacial grey pollinose. Border of lower calypter hyaline. Abdomen with blue pollinosity very faint. Head as in Fig. 36. Eyes at level of anterior ocellus separated by 0.40 of head width. Fore femur on anterior and anteroventral surfaces with complete rows of bristles. Mid tibia on dorsal surface with one preapical bristle, with apex not modified. Hind femur not modified.

Terminalia: Ovipositor as in Figs. 37 and 38. Spermathecae oval, with long ducts (Fig. 39).

Material examined.—Stein (1911) described this species from 4 pairs from Peru (Oroya). 4 ♂ and 3 ♀ syntypes have been studied as follows (all material listed in the original description is said to be from 21.i.04): PERU, Oroya, 21.i.04 4 ♂ (SMT); 30.v.04 1 ♀ (SMT); 22.i.04, 2 ♀ (SMT).



Figs. 37–43. 37–39. *Thaumasiochaeta nigriceps*. 37, Ovipositor (dorsal view). 38, Ovipositor (ventral view). 39, Spermatheca. 40–43. *T. compressitarsis*. 40, Male head (profile). 41, Male hind leg, anterior view. 42, Male sternite 5. 43, Cercal plate and surstyli (dorsal view).

Thaumasiochaeta compressitarsis (Stein), **new combination**
(Figs. 40–46)

Rhyncholimnophora compressitarsis Stein 1911: 142.

Diagnosis.—Male with fore tibia with bristles on anterodorsal, anterior and posterodorsal surfaces, dorsal surface with a long bristle near apex.

Differs from *T. pilitarsis* as follows:

Male—Body length: 3.5 mm; wing: 4.0 mm.

Color: Calypter whitish. Haltere with stalk yellow and knob yellowish brown.

Head: As in Fig. 40. Eyes at level of anterior ocellus separated by 0.30 of head width. Antenna with flagellomere 1.7 as long as pedicel.

Thorax: Fore leg as in Fig. 41. Fore femur on anterodorsal, anterior and anteroventral surfaces with complete rows of bristles; on anteroventral, ventral and posteroventral surfaces with strong bristles on apical half, forming a distinct group of bristles. Fore tibia with bristles on anterodorsal, anterior and posterodorsal surfaces, dorsal surface with a long bristle near apex. Fore tarsomere I on anterodorsal and posterodorsal surfaces with short strong bristles at apex. Mid femur on anterior surface with a row of bristles on basal half, posteroventral surface with a row of bristles on apical half. Mid tibia on anterior surface with 2 bristles on middle third, posterodorsal surface with a row of bristles on basal half; anteroventral surface with 4 short strong bristles on middle third; all surfaces with an apical bristle, those on anteroventral and anterodorsal surfaces longer. Hind femur curved in basal half; dorsal, anterodorsal, anterior and anteroventral surfaces with long, fine and sparse bristles on apical half. Hind tibia on anterior surface with 2 bristles on middle third; anterodorsal surface with a short preapical bristle; ventral surface with a strong apical bristle.

Abdomen: Tergite 3 with a pair of lateral marginal bristles, tergite 4 with a distinct marginal row of bristles and tergite 5 with a discal row of bristles. Sternite 5 longer than wide (Fig. 42).

Terminalia: Cercal plate with a deep posterior incision (Fig. 43); paramere with many sensillae at apex (Fig. 44).

Female.—Body length: 3.5 mm. Wing length: 3.0 mm.

Differs from male as follows: all brisles less strong than in male. Fore femur without the differentiated bristles on apical half of anteroventral, ventral and posteroventral surfaces. Fore tibia without the 2 long bristles at apex of dorsal surface. Mid tibia on anteroventral surface with 2 bristles on middle third; anterodorsal surface with 4 bristles on middle third; posteroventral surface with 2–3 bristles on middle third, posterior surface with 2 bristles on middle third. Hind femur not modified. Hind tibia on anteroventral surface with about 3–4 bristles on apical two-thirds, anterodorsal surface with 3–4 bristles on basal half. Hind tarsomere I without bristles at apex of anterodorsal and posterodorsal surfaces.

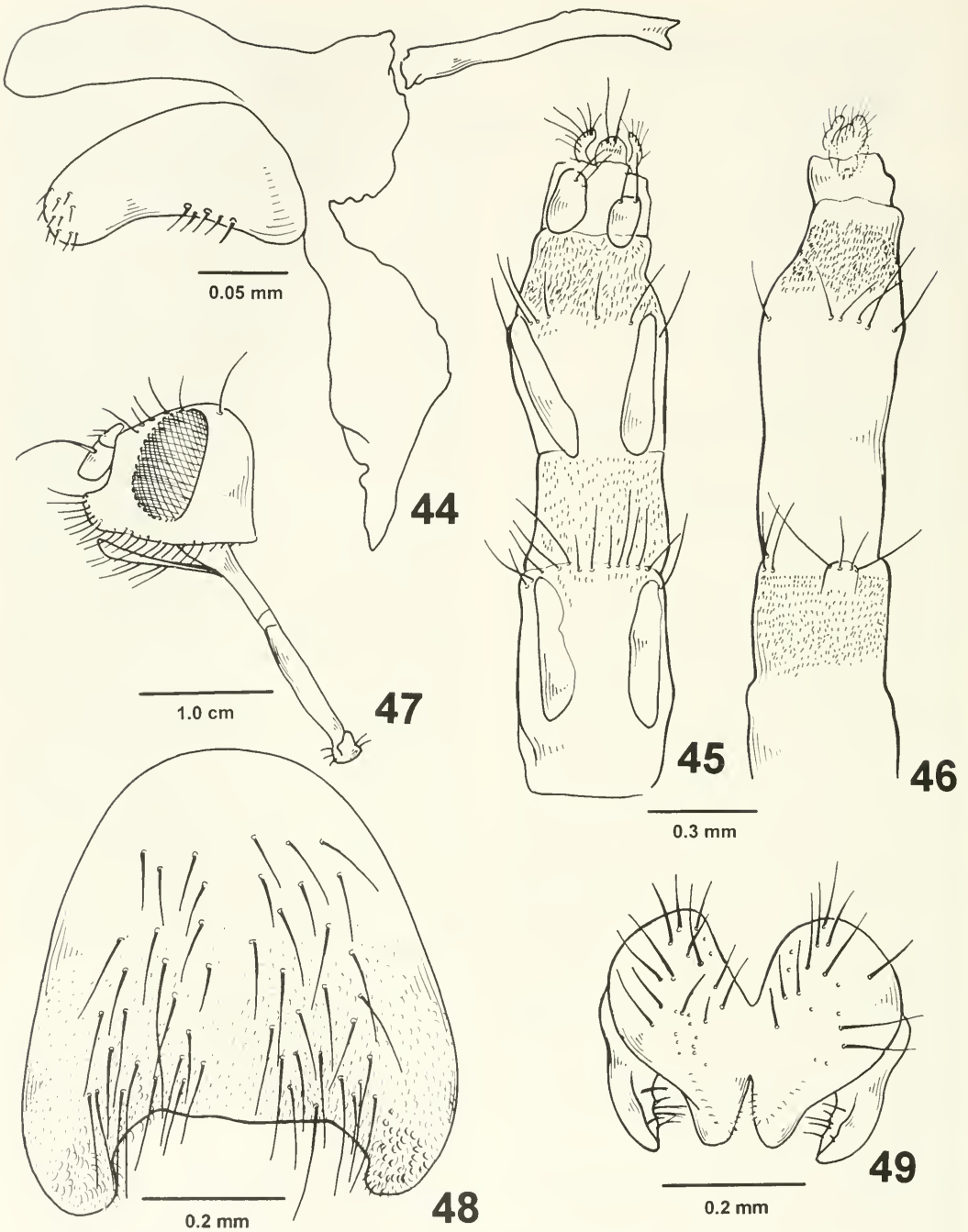
Terminalia: Ovipositor with cerci long, reaching beyond hypoproct (Figs. 45–46).

Material examined.—Stein (1911) described this species from only 4 ♂ and 3 ♀ from Peru (Vale de la Laris). 3 ♂ and 3 ♀ syntypes have been studied as follows: PERU, Laristhal, 8.viii.03, 1 ♂ (ZMHU); (Schnuse) 2 ♂ and 3 ♀ (SMT).

Thaumasiochaeta haustellata (Stein), **new combination**
(Figs. 47–50)

Rhyncholimnophora haustellata Stein 1911: 143.

Diagnosis.—Epistoma strongly projecting (Fig. 47). Ocellar triangle with only one pair of bristles. Calypter whitish. Hind femur on anteroventral, anterodorsal and anterior surfaces with sparse bristles. Hind tibia on anterodorsal and posterodorsal surfaces with 3 bristles on middle third, at the same level; anteroventral surface with 2 bristles on middle third; dorsal surface with



Figs. 44–49. 44–46. *Thaumasiochaeta compressitarsis*. 44, aedeagus (lateral view). 45, Ovipositor (dorsal view). 46, Ovipositor (ventral view). 47–49. *T. haustellata*. 47, Male head (profile). 48, Male sternite 5. 49, Cercal plate and surstyli (dorsal view).

a preapical bristle; anteroventral and ventral surfaces with an apical bristle.

Differs from *T. pilitarsis* as follows:

Male.—Length: body: 4.5 mm; wing: 4.2 mm.

Color: Calypter whitish. Fronto-orbital plates strongly grey pollinose from certain angles.

Head: Gena strongly projecting (Fig. 47). Ocellar triangle with only one pair of bristles.

Thorax: Fore femur on anterior, anteroventral and posterodorsal surfaces with complete rows of bristles. Fore tibia on dorsal surface with a preapical bristle; anteroventral, ventral and posteroventral surfaces with an apical bristle. Tarsi without differentiated bristles. Mid femur on posteroventral surface with sparse bristles on basal half. Mid tibia on anterodorsal surface with a long median bristle, 2 shorter ones on middle third, anteroventral surface with a short median bristle, posterior surface with 2 bristles on middle third; anterior, anterodorsal, posterodorsal, ventral and posteroventral surfaces with an apical bristle. Hind femur on anteroventral, anterodorsal and anterior surfaces with sparse bristles. Hind tibia on anterodorsal and posterodorsal surfaces with 3 bristles in middle third, at the same level; anteroventral surface with 2 bristles on middle third; dorsal surface with a preapical bristle; anteroventral and ventral surfaces with an apical bristle.

Abdomen: Sternite 5 longer than wide (Fig. 48).

Terminalia: Cercal plate and surstyli as in Fig. 49. Aedeagus with paramere broad, with no sensillae at apex (Fig. 50).

Material examined.—The only male from the original series was examined, as follows: PERU, Cuzco, 17.vi.05 1 ♂ (SMT).

Thaumasiochaeta longipalpis (Stein), **new combination**
(Figs. 51–55)

Rhyncholimnophora longipalpis Stein 1911: 143.

Diagnosis.—Epistoma very strongly projecting (Fig. 51). Ocellar triangle with only one pair of bristles. R_{4+5} on dorsal surface with setulae from base to r-m.

Differs from *T. pilitarsis* as follows:

Male.—Length: body: 5.3–5.6 mm; wing: 4.8–5.0 mm

Color: Male dark brown, female with fronto-orbital plates and gena silvery pollinose.

Head: Epistoma strongly projecting (Fig. 51). Ocellar triangle with only one pair of bristles.

Thorax: R_{4+5} on dorsal surface with setulae from base to r-m. Fore femur on anterior, anteroventral and anterodorsal surfaces with complete rows of bristles. Fore tibia on anterodorsal surface with one median bristle. Mid femur on posteroventral surface with a row of bristles on apical half. Mid tibia on anterodorsal surface with 3 bristles on middle third, posterior surface with 2 bristles on middle third, ventral surface with a long and strong apical bristle. Hind femur on anterodorsal, dorsal and anteroventral surfaces with complete rows of bristles. Hind tibia on anteroventral surface with 2 bristles on middle third and one preapical bristle, anterodorsal surface with 3 bristles on middle third; posterodorsal surface with a row of bristles on apical third; dorsal surface with a preapical long bristle.

Abdomen: Sternite 5 with many microtrichia on posterior membrane (Fig. 52).

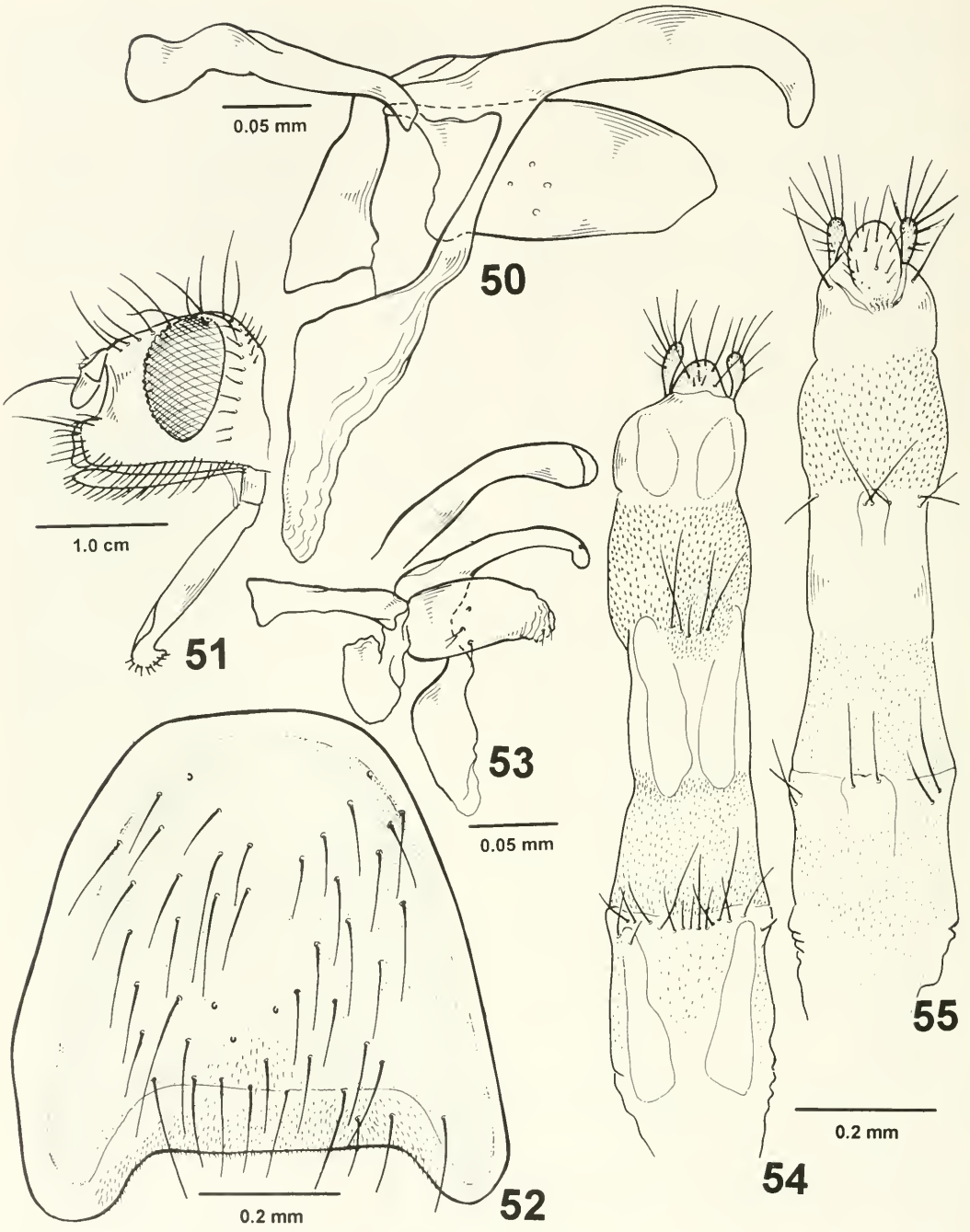
Terminalia: Cercal plate with a deep incision posteriorly; surstyli thinner at middle. Aedeagus with phallapodeme short, apex of paramere with few sensillae (Fig. 53).

Female.—Length: body: 5.2–5.5 mm; wing: 4.8–5.0 mm.

Differs from male as follows:

Terminalia: Ovipositor with microtrichia on all segments, except 7, where there are spicules (Figs. 54–55).

Material examined.—Stein (1911) described this species from 2 ♂ and 5 ♀ from



Figs. 50–55. 50, *Thaumasiochaeta haustellata* Aedeagus (lateral view). 51–55. *T. longipalpis*. 51, Male head (profile). 52, Male sternite 5. 53, Aedeagus (lateral view). 54, Ovipositor (dorsal view). 55, Ovipositor (ventral view).

Peru (Oroya). PERU (Oroya), 22.i.04 1 ♂ (ZMHU), (Schnuse) 1 ♂ and 3 ♀ (SMT).

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COMPARATIVE MORPHOLOGICAL ANALYSIS OF TESTIS FOLLICLES IN DUNG BEETLES (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE, APHODIINAE, GEOTRUPINAE)

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Abstract.—Testis follicles and sperm size of various Scarabaeinae, Aphodiinae, and Geotrupinae species were compared. Geotrupinae and Scarabaeinae species have 6 follicles per testis, except *Digitonthophagus gazella,* which has 12. In Aphodiinae, depending on tribe, some species have 7 follicles per testis (Aphodiini), with all follicles of the same size or with 2 large and 5 small follicles; other Aphodiinae (Eupariini) have only 2 follicles per testis. In Scarabaeinae and Aphodiinae, the follicles are not septate, while in Geotrupinae they are. Scarabaeinae spermatozoa measure from 90 to 600 μm, Geotrupinae spermatozoa from 116 a 166 μm. Aphodiinae spermatozoa length varies notably from tribe to tribe—in Aphodiini, from 500 to 2,000 μm, in Eupariini from only 110 to180 μm.

Resumen.—En varias especies de Scarabaeinae, Aphodiinae y Geotrupinae se estudiaron comparativamente los folículos testiculares y los espermatozoides. En Geotrupinae y Scarabaeinae hay seis folículos por testículo excepto en *Digitonthophagus gazella* que tiene doce. Mientras que en Aphodiinae, según la tribu, puede haber siete folículos por testículo del mismo tamaño o de dos tamaños: dos grandes y cinco pequeños (Aphodiini) o sólo dos folículos por testículo (Eupariini). En Scarabaeinae y Aphodiinae los folículos no son septados, mientras que en Geotrupinae son septados. Los espermatozoides en Scarabaeinae miden de 90 a 600 μm. En Geotrupinae miden de 116 a 166 μm. En Aphodiinae la longitud de los espermatozoides es muy diferente de una tribu a otra, en Aphodiini los espermatozoides miden de 500 a 2,000 μm y en Eupariini sólo de 110 a 180 μm.

Key Words: dung beetles, testis follicles, spermatozoa, escarabajos coprófagos, folículo testicular, espermatozoides

Most dung beetles of the subfamilies Scarabaeinae, Aphodiinae, and Geotrupinae depend on the excrement of herbivores, owing to these beetles' feeding and reproductive behaviors. Dung is used for nesting and depositing eggs, and as food for both developing and adult individuals. For these reasons, dung beetles play a critical role in maintaining grasslands: in using dung, they reduce its presence on the ground, prevent the loss of elements like nitrogen that the dung contains, and increase soil fertility (Halffter and Mathews 1966, Halffter and Edmonds 1982, Rougon et al. 1988, Hanski and Cambefort 1991).

The anatomy and morphology of male genitalia of many species in these subfamilies have been studied for taxonomic purposes (Sharp and Muir 1912, Zunino 1983, 1984, D'Hotman and Scholtz 1990). Nev-

ertheless, few aspects of the internal structure of testis follicles are known for some Scarabaeinae species (Virkki 1956, 1957, Benítez and Martínez 1985, Martínez and Benítez 1988, Martínez and Cruz 1992). There is also a lack of information on Aphodiinae (Virkki 1951, 1953, 1956, 1957) and Geotrupinae (Virkki 1951, 1956, 1957, López-Guerrero and Benítez 1982, López-Guerrero 1987). Nothing about the spermatozoa of any of these species has been studied previously.

Given the biological and ecological importance of these subfamilies and the lack of knowledge about male reproductive anatomy among their species, the present investigation made a comparative analysis of the microscopic structure of testis follicles and spermatozoa size in various species of Scarabaeinae, Aphodiinae, and Geotrupinae.

Materials and Methods

A number of dung beetle species were studied, representing the principal tribes of the three subfamilies. Most of these species were collected in Mexico, some in France and Uruguay. The species studied were as follows:

Scarabaeinae (*sensu* Halffter 1997): Onthophagini: *Onthophagus batesi* Howden and Cartwright, *O. chevrolati* Harold, *O. incensus* Say, *O. cyanellus* Bates, *O. rhinolophus* Harold, *O. hippopotamus* Harold, *O. aureofuscus* Bates, and *Digitonthophagus gazella* (Fabricius). Onitini, Gromphina: *Gromphas lacordairei* (Brullé). Phanaeina: *Phanaeus tridens* Laporte, *P. amethystinus* Harold, *P. endymion* Harold, *P. damon* Castelnau, *Coprophanaeus telamon* (Harold), *C. pluto* (Harold), and *Sulcophanaeus menelas* Laporte. Oniticellini, Oniticellina: *Euoniticellus intermedius* (Reiche) and *Liatongus rhinocerulus* (Bates). Coprini, Coprina: *Copris laeviceps* Harold, *C. incertus* Say, *C. lugubris* Boheman, *C. armatus* Harold, and *C. klugi sierrensis* Matthews. Dichotomiina: *Dichotomius satanas* (Harold), *D. carolinus* (Say), *D. centralis* (Harold), *Canthidium moestum* Harold, *Ateuchus illaesum* Harold, and *Ontherus mexicanus* Harold. Eurysternini: *Eurysternus mexicanus* Harold and *E. caribaeus* (Herbst). Scarabaeini, Canthonina: *Canthon indigaceus chevrolati* Harold, *C. i. chiapas* Robinson, *C. cyanellus cyanellus* LeConte, *C. viridis viridis* Martínez, Halffter, and Halffter, *C. humectus* (Say), *C. (Glaphyrocanthon) femoralis femoralis* Chevrolat, *C. (G.) viridis leechi* Martínez, Halffter and Halffter, *C.(G.) subhyalinus* Harold, *Deltochilum pseudoparile* Paulian, *D. lobipes* Bates, and *D. gibbosum* (Fabricius).

Aphodiinae (*sensu* Endrödi 1966): Aphodiini: *Aphodius (Teuchestes) fossor* (L.), *A. (Colobopterus) erraticus* (L.), *A. (Calamosternus) granarius* (L.), *A. (Labarrus) pseudolividus* Balthasar, *A. (Trichaphodius) opisthius* Bates, *A. (Platyderides) fuliginosus* Harold, and *A. (Bodilus) sallei* Harold. Eupariini: *Ataenius cribrithorax* Bates, *A. sculptor* Harold, *A. sp. aff. perforatus* Harold, *A. sp. aff. cognatus* LeConte.

Geotrupinae (*sensu* Zunino 1984): Geotrupini: *Megatrupes cavicollis* Bates, *Anoplotrupes stercorosus* (Scriba), and *Trypocopris vernalis* (L.). Ceratotrupini: *Halffterius rufoclavatus* (Jekel), *Ceratotrupes bolivari* Halffter and Martínez, *Onthotrupes herbeus* (Jekel), *O. sobrinus* (Jekel), and *O. nebularum* (Howden).

For each species, 5 to 10 males were dissected in Ringer solution, and their reproductive apparatus fixed in AFATD (ethyl alcohol 96°–formaldehyde–trichloroacetic acid–dimethylsulfoxide) (Carayon 1969). To study the structure of the testicular follicles, most were stained with Feulgen-green light and mounted in their entirety. Other follicles were imbedded in Histosec®, and histological sections of 7 μm were stained with PAS-Hematoxylin (Gabe 1968). To study spermatozoa, a follicle smear was taken from mature males, fixed in methanol, and stained with Giemsa (Clark 1973).

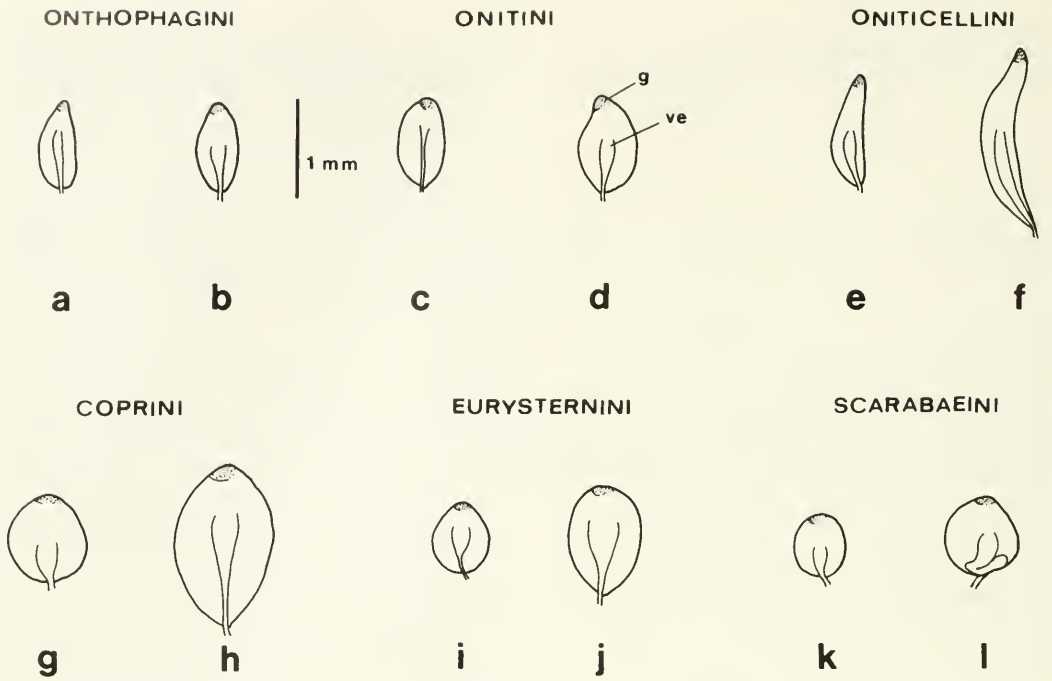

Fig. 1. Schematics of testis follicle forms in species of the principal Scarabaeinae tribes. Onthophagini: a, *Onthophagus batesi*; b, *Digitonthophagus gazella*. Onitini: c, *Gromphas lacordairei*; d, *Phanaeus tridens*. Oniticellini: e, *Euoniticellus intermedius*; f, *Liatongus rhinocerulus*. Coprini: g, *Copris incertus*; h, *Dichotomius satanas*. Eurysternini: i, *Eurysternus mexicanus;* j, *Eurysternus caribaeus*. Scarabaeini: k, *Canthon indigaceus chevrolati*; l, *Deltochilum pseudoparile*. (g = germarium; ve = vas efferens).

Results

Scarabaeinae

Males of the Scarabaeinae have two testes, each with six follicles, with the exception of *D. gazella,* which has 12 follicles per testis (Pluot-Sigwalt and Martínez 1998). The form of the follicles is variable—they can be spherical, ovoids, or very elongated ovoids (Fig. 1)—and their coloration *in vivo* varies with species, independently of sexual maturity.

In Onthophagini (Figs. 1a, b), follicles can be very elongated ovoids, either white (*Onthophagus batesi, O. incensus, O. cyanellus, O. rhinolophus*) or yellowish (*O. chevrolati, O. hippopotamus, D. gazella*). In Onitini (Figs. 1c, d), they are ovoids, yellowish (*Phanaeus tridens, P. demon, P. amethystinus, Coprophanaues pluto, Gromphas lacordairei*) or orangish (*P. endymion, C. telamon, Sulcophanaeus menelas*). In Oniticellini (Figs. 1e, f), they can be very elongated white ovoids (*Euoniticellus intermedius, Liatongus rhinocerulus*). Coprini Coprina (Fig. 1g) follicles can be spherical, whether white (*Copris incertus, C. armatus, C. klugi sierrensis*), yellowish (*C. laeviceps*), or orangish (*C. lugubris*); while in Dichotomiina (Fig. 1h), follicles are ovoids, whether orangish (*Dichotomius satanas, D. carolinus, D. centralis*), yellowish (*Canthidium moestum*), or white (*Ateuchus illaesum, Ontherus mexicanus*). Eurysternini (Figs. 1i, j) present elongated ovoids that are white (*Eurysternus mexicanus*) or yellow (*E. caribaeus*). Scarabaeini (Figs. 1k, l) follicles are spherical, either white (*Canthon cyanellus cyanellus, C. viridis viridis, C. humectus*), yellowish (*C. [Glaphyrocanthon] femoralis femoralis, C. [G.] viridis leechi, C. [G.] subhyalinus, Deltochilum gibbosum*), or orangish (*Canthon indiga-*

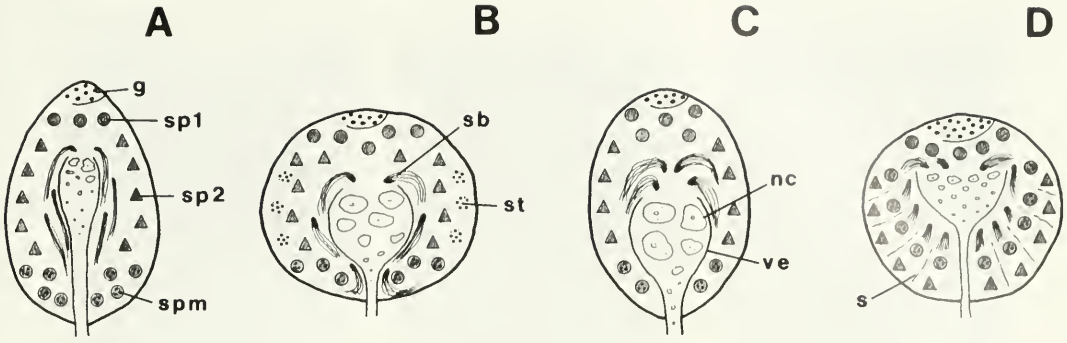

Fig. 2. General scheme of testis follicle structure in A, Scarabaeinae; B, Aphodiini; C, Eupariini; D, Geotrupinae. (g = germarium; nc = nurse cells; s = septa; sb = sperm bundles; sp1 = primary spermatocytes; sp2 = secondary spermatocytes; spm = spermatids; st = spermatozoa tails, transverse sections; ve = vas efferens).

ceus chevrolati, C. i.chiapas, D. pseudoparile, D. lobipes). The follicles of Dichotomiina and Eurysternini are notable for their strong similarity to each other.

In all the Scarabaeinae species studied, each follicle shows radial symmetry and is externally defined by a cellular wall. In the apical region, the germarium is separated from other follicular tissue by an acellular membrane; in the central region, the vas efferens is found, and around the vas efferens, cysts in different spermatogenesis stages (Figs. 2A, 3A).

The cellular wall that defines each follicle varies in thickness according to the species, with the thickest walls seen in *C. telamon, D. satanas, E. caribaeus,* and *D. gibbosum.* In all Scarabaeinae species, the germarium contains abundant spermatogonia. The vas efferens begins relatively close to the germarium and is straight, taking the form of a funnel, with the anterior region open and more enlarged than the posterior region. Inside the vas efferens, in mature males, are abundant nurse cells and sperm bundles. Upon leaving the follicles, the vas efferens narrows until it joins the vas deferens. Depending on tribe, the anterior part of the vas efferens can be more or less enlarged, while the posterior region is straight, except in the genus *Deltochilum,* in which it is bent toward the base of the follicle (Fig. 1,l). The nurse cells in the vas efferens of mature males measure 22 to 66 μm in diameter, depending on species (Figs. 3A, B, C).

The arrangement of cysts in different maturational stages is constant within any tribe. Cysts of spermatogonia and primary spermatocytes are located under the germarium. Secondary spermatocyte cysts migrate toward the periphery, from the anterior to the posterior region of the follicle. Spermatid cysts are found in the posterior and central region of the follicle and toward the posterior part of the vas efferens. Maturing sperm adhere to nurse cells and are found around the vas efferens from the posterior to the anterior region. The nurse cells have a strong PAS+ reaction.

Sperm bundles are generally found parallel to the direction of the vas efferens in long ovoid follicles, or in an irregular pattern of spherical or ovoid follicles. They occur abundantly at the entrance of the vas efferens and within it, where they are found free among degenerating nurse cells (Figs. 2A, 3A, B, C). Within the sperm bundles of most species, spermatozoa tails are elongated and do not undulate much, but they can also be found balled up, as in *C. telamon, G. lacordairei, D. satanas, C. moestum,* and *A. illaesum,* or in a zig-zag form, as in *P. tridens* and *D. carolinus.*

Spermatozoa are tailed in all species of this subfamily. Cell length varies from 90 to 600 μm, depending on tribe. In Onthophagini species, spermatozoa length is 320

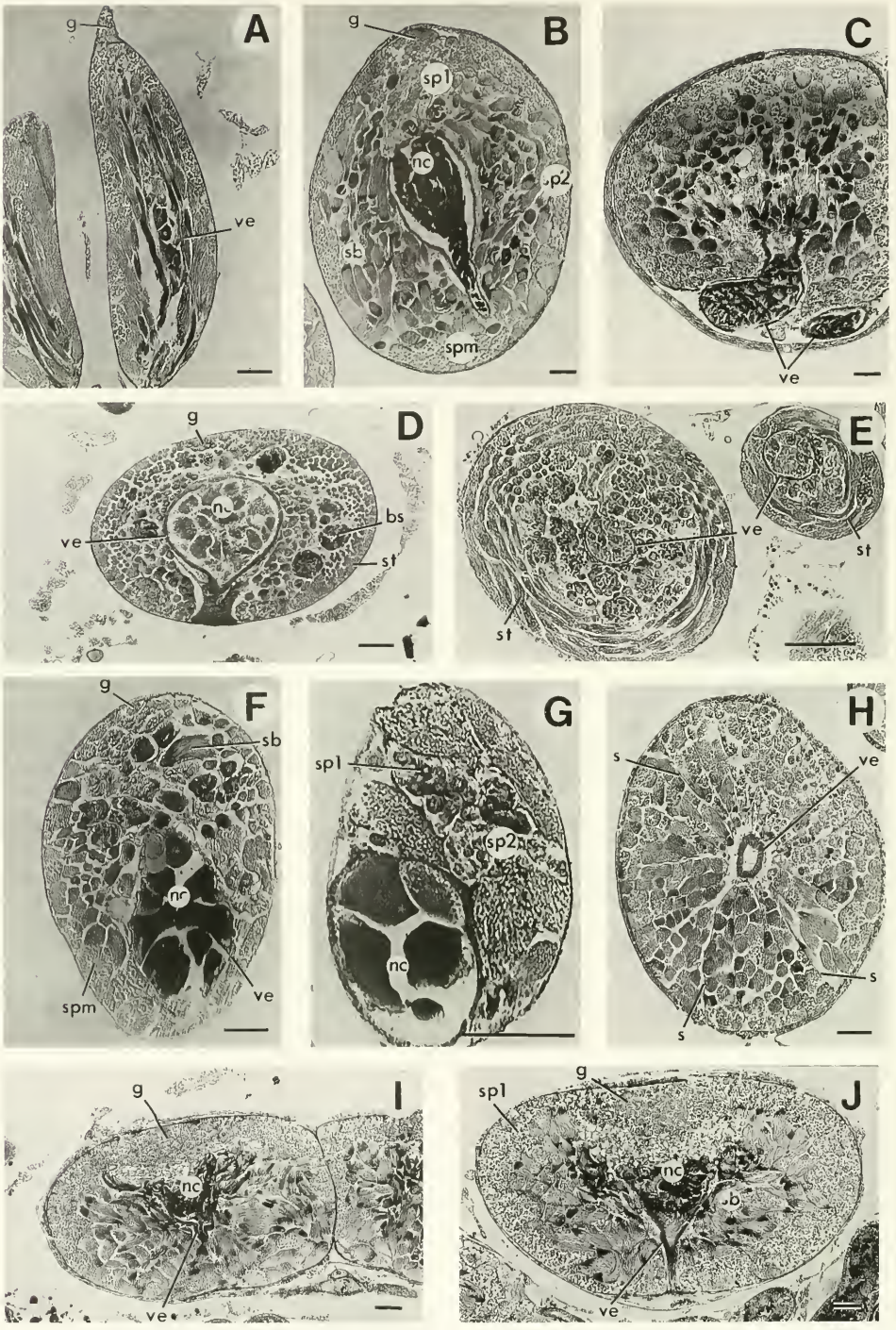

Fig. 3. Microphotographs of histological sections of the testis follicles of species in the three subfamilies. Scarabaeinae: longitudinal sections in A, *Onthophagus batesi*; B, *Eurysternus caribaeus* and C, *Deltochilum gibbosum*. Aphodiinae, Aphodiini: D, *Aphodius fossor* in longitudinal section and E, *Aphodius sallei*, follicles of two different sizes in transverse section. Eupariini: longitudinal sections in F, *Ataenius sculptor* and G, *Ataenius cribrithorax*. Geotrupinae: H, *Anoplotrupes stercorosus* in transverse section and longitudinal sections

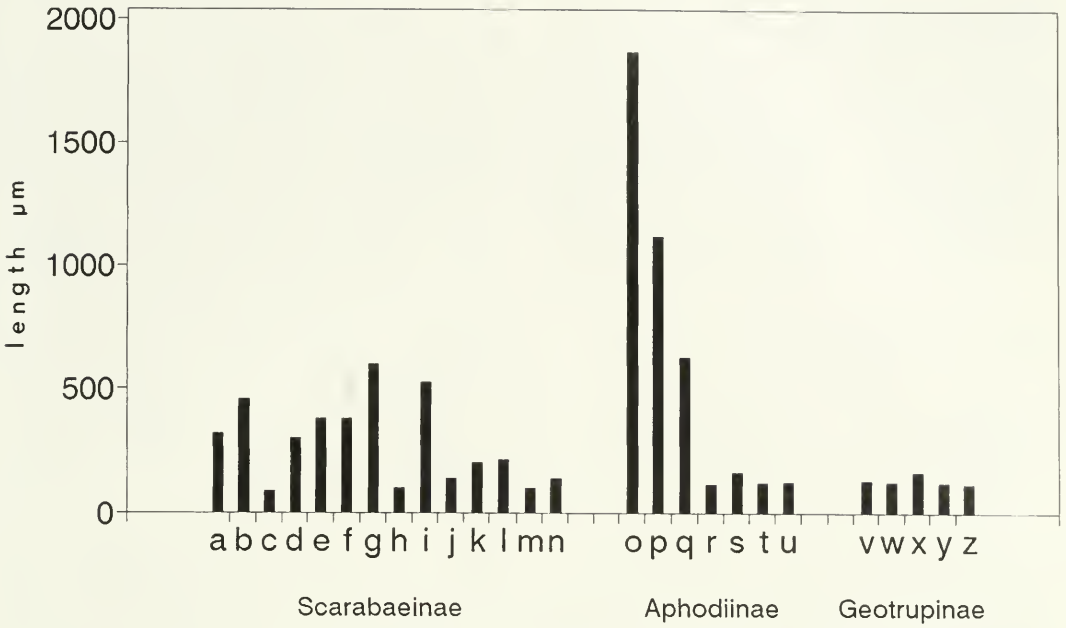

Fig. 4. Graph illustrating spermatozoa size in species of the three subfamilies. Scarabaeinae: a, *Onthophagus batesi*; b, *Onthophagus cyanellus*; c, *Digitonthophagus gazella*; d, *Phanaeus amethystinus*; e, *Sulcophanaeus menelas*; f, *Euoniticellus intermedius*; g, *Liatongus rhinocerulus*; h, *Copris laeviceps*; i, *Dichotomius carolinus*; j, *Ontherus mexicanus*; k, *Eurysternus mexicanus*; l, *Eurysternus caribaeus*; m, *Canthon cyanellus cyanellus*; n, *Deltochilum pseudoparile*. Aphodiinae: o, *Aphodius opisthius*; p, *Aphodius sallei*, spermatozoa from the large follicle; q, *Aphodius sallei*, spermatozoa from the small follicle; r, *Ataenius cribrithorax*; s, *Ataenius sculptor*; t, *Ataenius sp. aff. perforatus*; u, *Ataenius sp. aff. cognatus*. Geotrupinae: v, *Anoplotrupes stercorosus*; w, *Megatrupes cavicollis*; x, *Ceratotrupes bolivari*; y, *Onthotrupes nebularum*; z, *Halffterius rufoclavatus*.

to 460 µm, except in *D. gazella*, whose much smaller spermatozoa measure about 90 µm (Figs. 4a, b, c). In Onitini, spermatozoa length is 300 to 380 µm. The shortest spermatozoa are found in *P. amethystinus* and *C. pluto*, the longest in *S. menelas* (Figs. 4d, e). Among Oniticellini species, the spermatozoa length of *E. intermedius* is about 380 µm, that of *L. rhinocerulus* 600 µm (Figs. 4f, g). In Coprini Coprina, spermatozoa measure between 100 and 120 µm (Fig. 4h). For Dichotomiina, spermatozoa length is from 320 to 530 µm (as in *D. carolinus*), except in *O. mexicanus*, which has a spermatozoa length of 140 µm (Figs. 4i ,j). In the two Eurysternini species, spermatozoa length is about 200 µm (Figs. 4k, l). Scarabaeini Canthonina species have spermatozoa lengths from 100 to 160 µm (Figs. 4m, n).

Aphodiinae

In Aphodiinae, the number of testes follicles varies with tribe (Pluot-Sigwalt and Martínez 1998). Males of the Aphodiini tribe have seven spherical white follicles in each of two testes. In some of these species, all seven follicles are of the same size (*A. fossor, A. opisthius*); in others, there are two large follicles and five smaller follicles,

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in I, *Onthotrupes sobrinus* and J, *Onthotrupes nebularum*. (bs = balled sperm bundles; g = germarium; nc = nurse cells; s = septa; sb = sperm bundles; sp1 = primary spermatocytes; sp2 = secondary spermatocytes; spm = spermatids; st = spermatozoa tails; ve = vas efferens). The scale represents 100µm.

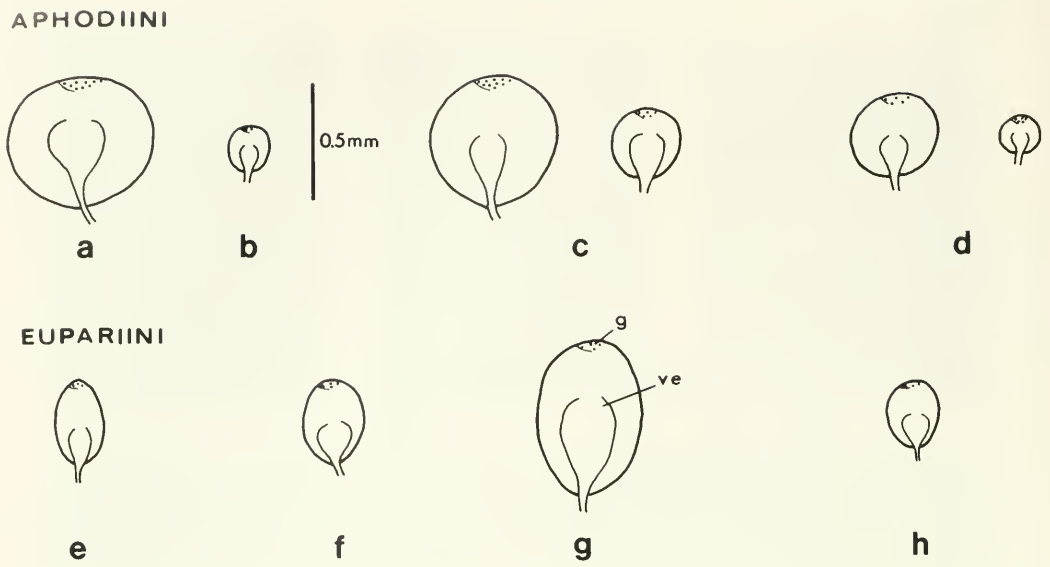

Fig. 5. Schemes showing the form of testis follicles in the two Aphodiinae tribes. Aphodiini with follicles of the same size: a, *Aphodius fossor*; b, *Aphodius opisthius*. Aphodiinae with two sizes of follicle: c, *Aphodius fuliginosus*; d, *Aphodius pseudolividus*. Eupariini: e, *Ataenius cribrithorax*; f, *Ataenius sp. aff. perforatus*; g, *Ataenius sculptor*; h, *Ataenius sp. aff. cognatus*. (g = germarium; ve = vas efferens).

with the smaller follicles measuring about half the size of the larger ones (*A. erraticus, A. granarius, A. lividus, A. fuliginosus, A. sallei*). In contrast, Eupariini species have just two white, ovoid follicles of the same size in each testis (Fig. 5).

In Aphodiini species, each follicle, independent of its size, has an external cellular wall, a germarium in the apical region that is basally bounded by a membrane, and a central vas efferens with cysts in various states of development around it (Figs. 2B, C). The germarium contains few spermatogonia. The vas efferens takes the form of a capsule, which is very enlarged in the anterior region, and in mature males, contains large, degenerating nurse cells (Figs. 3D, F). All follicles, whether large or small, show a paucity of cysts in different stages of spermatogenesis, but these cysts are large. Follicles of both sizes are functional. Cyst distribution is roughly similar to that described for Scarabaeinae species. Beneath the germarium, toward the entrance of the vas efferens, are primary spermatocyte cysts that are large but few in number. Secondary spermatocyte cysts are found in the middle region of the follicle toward the periphery and in the posterior region. Spermatid cysts are present in the posterior region around the vas efferens. Young sperm bundles have spermatozoa with short tails, take the form of balls, and are grouped around the anterior part of the vas efferens. The most notable features of the Aphodiini species studied are the distribution of mature sperm bundles and spermatozoa size. Sperm bundles are located around the vas efferens, but spermatozoa tails are so long that they curl up several times before meeting the periphery, and thus are found under the follicle wall from the apical to the basal region of the follicle. In a longitudinal section of the follicle, the spermatozoa tails under the follicle wall are therefore seen cut transversely (Figs. 2B, 3D, E). Nurse cells found in the vas efferens measure from 17 to 50 μm in diameter (Figs. 3D, E).

Aphodius opisthius follicles are about the same size, measuring about 215 μm in diameter, and their spermatozoa measure approximately 2,000 μm. Species with folli-

cles of two different sizes, such as *A. sallei,* with 2 follicles measuring about 300 μm in diameter and 5 follicles measuring about 150 μm in diameter, have spermatozoa of two different sizes. In these species, large-follicle spermatozoa are about 1,000 μm in length, while small-follicle spermatozoa measure about 500 μm (Figs. 4o, p, q).

Testis follicles of Eupariini species follow the same general scheme as in Aphodiini (Fig. 2C). These species also have large but few cysts in various maturational stages. Sperm bundles are found around the entrance of the vas efferens, but they are not beneath the follicle wall. Balled sperm bundles are also observed, but in lesser quantity than in Aphodiini. The nurse cells found within the vas efferens are very large, from 49 to 93 μm in diameter (Fig. 3F). The spermatozoa measure only 110 to 200 μm in length (Figs. 4r, s, t, u).

Geotrupinae

Males of the Geotrupinae subfamily have two testes, with six follicles in each (Pluot-Sigwalt and Martínez 1998). The follicles are spherical and white in all the species studied (Fig. 6).

In species of the two Geotrupinae tribes, follicles have a thick external cellular wall, a relatively large germarium with abundant spermatogonia, and a vas efferens, with abundant cysts in different stages of development. In both tribes, testis follicles have radially organized septa, with the septa more notable in Geotrupini than in Ceratotrupini. The vas efferens begins very close to the germarium and has a conical form, with a very open anterior region, and a thick wall in the posterior region (Figs. 2D, 3G, H).

Because of the presence of septa, the distribution of cysts is very different from that observed in Scarabaeinae and Aphodiinae. Cysts of primary spermatocytes are found beneath the germarium and beneath the follicle wall. Found in each septa, toward the center of the follicle, are secondary spermatocyte cysts, spermatid cysts, and sperm bundles. Within the entrance of the vas efferens, abundant sperm bundles are found together with nurse cells. Within the vas efferens itself are numerous degenerating nurse cells, measuring 17 to 20 μm in diameter (Figs. 3G, H). Spermatozoa length does not vary much in Geotrupini and Ceratotrupini species—from 116 a 166 μm (Figs. 4v, w, x, y, z).

Comparison of the Subfamilies and Discussion

These observations of testis follicles and spermatozoa size in Scarabaeinae, Aphodiinae, and Geotrupinae show that both similarities and differences are found at the levels of subfamily, tribe, and genus.

Morphology of testis follicles.—The form of testis follicles varies according to subfamily, and in some subfamilies, according to tribe (Figs. 1, 5, 6). The greatest variation in tribes was seen in Scarabaeinae, whose follicles vary from elongated ovoids to spheres. The most elongated follicles of all were seen in Onthophagini and Oniticellini, the most spherical in Coprini and Canthonina. In Aphodiinae, ovoid follicles are seen in Eupariini, and spherical follicles in Aphodiini. In the two Geotrupinae tribes, follicles are spherical. According to Virkki (1957), long ovoid follicles are more primitive than spherical ones. From this perspective, in Scarabaeinae the most primitive follicle state would be those of Onthophagini and Oniticellini, and the most evolved in Coprini and Canthonina. In Aphodiinae, the most evolved follicles would be those of Aphodiini. In Geotrupinae, no differences are seen: both of the two tribes have spherical follicles.

Microscopic structure of testis follicles.—The microscopic structure of testis follicles is similar in Scarabaeinae and Aphodiinae, but quite different in Geotrupinae (Figs. 2, 3). The follicles are not septate in Scarabaeinae and Aphodiinae, while in Geotrupinae they are—differences that Virkki (1951, 1957) had already observed in some species among these subfamilies.

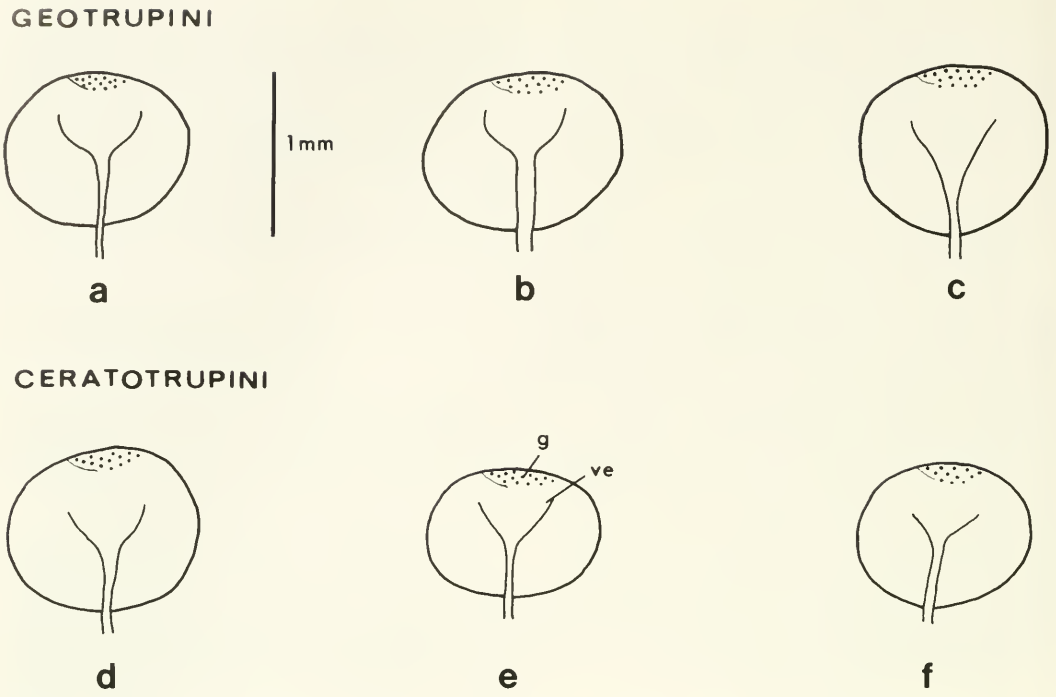

Fig. 6. Schemes of testis follicles in the two Geotrupinae tribes. Geotrupini: a, *Megatrupes cavicollis*; b, *Trypocopris vernalis*; c, *Anoplotrupes stercorosus*. Ceratotrupini: d, *Ceratotrupes bolivari*; e, *Onthotrupes nebularum*; f, *Halffterius rufoclavatus*. (g = germarium; ve = vas efferens).

Similarly, the distribution of cysts in different stages of spermatogenesis is similar in Scarabaeinae and Aphodiinae, but distinct in Geotrupinae. Nevertheless, in Scarabaeinae and Geotrupinae the germarium contains abundant sperm, while in Aphodiinae they are few. Again, cysts in different developmental stages are quite abundant in Scarabaeinae and Geotrupinae, and scarce in Aphodiinae. Another characteristic of Aphodiinae is that the primary spermatocytes are very large, a feature already described and analyzed by Virkki (1956, 1957). Largely for these reasons, Virkki (1951, 1957) considered *Aphodius* more evolved than Scarabaeinae species. Geotrupinae follicles present a structure like that of Melolonthinae and Rutelinae follicles (Virkki 1956, 1957).

Sperm bundles are distributed similarly in Scarabaeinae and Eupariini, but very differently in Aphodiini. One Aphodiini characteristic is that sperm bundles are found beneath the follicular wall, even in species that have two sizes of follicle. This type of distribution is not seen in Aphodiinae Eupariini, nor in Scarabaeinae or Geotrupinae. Virkki (1951, 1956, 1957) is the only author to have studied some Aphodiini species. However, he did not note the differences in follicle size among these species, nor the distribution of sperm bundles as described here. Eupariini have never been studied previously.

The presence of balled sperm bundles, which Virkki (1957) considers characteristic of Aphodiinae, was also observed in this study in some Scarabaeinae species: *C. telamon, G. lacordairei, D. satanas, C. moestum,* and *A. illaesum.* Balled sperm bundles were not seen in Geotrupinae.

Spermatozoa.—In Scarabaeinae species, spermatozoa measure from 90 to 600 μm in length. The longest Scarabaeinae spermatozoa (from 300 to 600 μm) are seen in Onthophagini species (except in *D. gazella,*

which has spermatozoa about 90 μm long), and in Onitini Oniticellina and Dichotomiina (except in *O. mexicanus,* whose spermatozoa are about 100 μm long). The shortest spermatozoa (from 100 to 200 μm) are found in Coprina, Eurysternina, and Canthonina.

The Aphodiinae subfamily shows the greatest variation in spermatozoa length from one tribe to another. In Aphodiini, spermatozoa measure between 500 and 2,000 μm. The spermatozoa about 2,000 μm long are found in species with just one follicle size. Species with two sizes of testis follicle have spermatozoa about 1,000 μm in length in the larger follicle, and about half that length in the smaller follicle. In contrast, in Eupariini, spermatozoa are just 110 to 180 μm.

In Geotrupinae, spermatozoa length is similar in both tribes: in Geotrupini, from 126 to 137 μm, and in Ceratotrupini, from 116 to 166 μm (Fig. 4).

With regard to body length, the Aphodiini studied, except for *A. fossor,* measure from 4 to 5 mm, and are thus the smallest of the three subfamilies. Scarabaeinae and Geotrupinae measure from 7 to 15 mm in body length. Nevertheless, Aphodiini have the largest spermatozoa, if the fewest. The characteristics observed in *Aphodius*—the unusual size of spermatozoa together with the form they take of being rolled up beneath the wall of the follicle, which is spherical and small (about 22 to 50 mm)—have been described in one other species of Coleoptera, *Alagoasa bicolor* (L.) (Chrysomelidae) by Virkki and Bruck (1994). Spermatozoa of large size have also been observed in other Coleoptera, such as *Divalves bipustulatus* (F.) (Cleridae) and *Ptinella aptera* (Guerin) (Ptiliidae), species in which spermatozoa measure double the length of the body (Mazzini 1976, Taylor et al. 1982); and in some species of Diptera, such as *Drosophila littoralis* Meigen, in which spermatozoa can measure up to 19 mm (Bressac et al. 1991). In Diptera, however, the organization of cysts during spermatogenesis is different from that in Coleoptera: the tubiform testes of *Drosophila* allows the parallel elongation of sperm bundles (Tokuyasu et al. 1972), which could not occur in *Aphodius* or *Alagoasa,* which have spherical follicles.

What might the advantages be of the fewer, longer spermatozoa for Aphodiinae? According to Virkki (1973), reduction in sperm bundles reflects the total production of spermatozoa, and specialized insects tend to have fewer sperm bundles than more primitive insects. Reduction in spermatozoa number probably limits genetic variability and facilitates the adaptation of populations to specialized niches.

Male dung beetles have been studied very little. There are only few scattered data for a small number of species on the morpho-functional aspects of their reproductive apparatus. The Scarabaeinae, Aphodiinae, and Geotrupinae males lack seminal vesicles; their spermatozoa accumulate in the vas deferens, which has a muscular wall; and they have an ejaculatory duct with thick muscular walls (Pluot-Sigwalt and Martínez 1998). During mating, Scarabaeinae males form a voluminous spermatophore (Cruz and Martínez 1992). In some Aphodiinae species, spermatophores have also been observed. In *A. opisthius* spermatozoa measure about 2,000 μm, and the females have a spermatheca that measures approximately 300 μm in length (Martínez, M. I., unpublished observations). Several questions are raised by these differences between the size of the spermatozoa and that of the spermatheca in which the spermatozoa are stored following mating. How do the very large spermatozoa pass from the testes to the spermatheca? And how are the spermatozoa accomodated within the spermatheca?

With regard to nesting, Scarabaeinae species show complex nesting behavior, with some species caring for the nest until the young emerge. In this sense, Scarabaeinae appear to be the most evolved; and they have the lowest fecundity. On the other

hand, Aphodiinae have the least evolved nesting behavior, and the females show the highest level of fecundity (Halffter and Edmonds 1982; Cambefort and Hanski 1991). What might the advantages be of the fewer, longer apermatozoa for Aphodiinae? According to Virkki (1973), reduction in sperm bundles reflects the total production of spermatozoa, and specialized insects tend to have fewer sperm bundles than more primitive insects. Reduction in spermatozoa number probably limits genetic variability and facilitates the adaptation of populations to specialized niches.

The questions that have been raised here define some of the next research steps about the reproductive biology of dung beetles, particularly the less well known Aphodiinae.

Acknowledgments

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A FOSSIL APHID (HEMIPTERA: STERNORRHYNCHA) IN DOMINICAN AMBER

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Abstract.—***Dominicaphis succini*, n. gen., n. sp.** is described from Dominican amber as a member of the Hormaphididae (Hemiptera: Sternorrhyncha). It resembles *Aleurodaphis blumeae* van der Goot (Hormaphididae) but also has characters in common with some members of the Eriosomatidae and may be close to the common ancestor of the two families.

Key Words: Dominican amber, fossil aphid, Hormaphididae, Eriosomatidae

Dominican amber contains numerous insects and other arthropods (Poinar 1992) but very few aphids. Only one aphid species has previously been described from this source, namely *Mindazerius dominicanus* Heie and Poinar (1988) (Drepanosiphidae: Lizerini). A second species representing a parthenogenetic viviparous female has now been found and is described below.

Materials and Methods

The fossil specimen, which occurs in a small piece of transparent yellow amber, is well preserved and undamaged (Fig. 1). A binocular Zeiss-Winkel microscope with a 10× objective was used for the description. Placing the amber piece in mineral oil facilitated microscopic observation.

The specimen is believed to have originated from mines in the Cordillera Septentrional of the Dominican Republic. These mines are in the El Mamey Formation (Upper Eocene), which is a shale-sandstone interspersed with a conglomerate of well-rounded pebbles (Eberle et al. 1980). The exact age of the amber is unknown, and estimates based on various microfossils and chemical analyses provide a range from 15–20 million years (Iturralde-Vincent and MacPhee 1996) to 30–45 years (Cepek in Schlee 1990). Dominican amber originated from leguminous trees of the genus *Hymenaea*, especially *H. protera* (Poinar 1991).

Dominicaphis Heie and Poinar, new genus

Description.—Antenna 5-segmented, with ring-shaped rhinaria. Fore wing with one media fork and cubitus-branches departing from main vein at same point. Hind wing with two well separated oblique veins. Mesothoracic lobes rather distinctly developed.

Type-species.—*Dominicaphis succini*, n. sp.

Etymology.—Derivation of name: Genus name derived from "Dominican" and *Aphis*.

Dominicaphis succini Heie and Poinar, new species

Description (all measurements in mm).—Alate specimen, probably a parthenogenetic viviparous female. Body 1.30 long, head

Fig. 1. *Dominicaphis succini* in dorsal view (length of body 1.3 mm).

0.22 long, abdomen 0.74 long, fore wing 1.90 long, hind wing 1.10 long. Head and thorax black, abdomen rather pale with some slightly darker fields; hairs apparently very short; frons straight; width of head across eyes 0.27, longitudinal diameter of compund eyes 0.10, ocular tubercles rather large, situated behind compound eyes, longitudinal diameter 0.04; antenna dark, 5-segmented, 0.50 long; lengths of segments: III = 0.19, IV = 0.09, V = 0.11; rhinaria linear to narrowly ring-shaped, primary and secondary rhinaria apparently similar, III with 14, IV with 5, V with 6 or perhaps 7; rostrum difficult to see, apparently very short, reaching to middle of prothorax. Mesothoracic lobes distinctly visible; femora black with paler bases, tibia with dark tips; lengths: fore femur 0.25, middle femur 0.27, hind femur 0.29, fore tibia 0.30, middle tibia 0.29, hind tibia 0.31, tarsi about 0.06–0.07; fore wing with slender, pointed pterostigma, radial sector departing from its distal half close to middle, media weaker than other veins, its basal part invisible, distance between point of media fork and cubitus branches and base of fore wing 0.54; hind wing with two well separated oblique veins; apical oblique vein rather long and forming a small angle with main vein. Abdomen rather broad in middle, width 0.50; details not distinctly visible; siphuncular pores invisible, perhaps present; cauda apparently rounded; a slightly visible pointed projection about 0.10 long situated below cauda.

Holotype.—Accession number HO-4-43, deposited in the Poinar Amber Collection maintained at Oregon State University, Corvallis, Oregon.

Etymology.—Derivation of specific name: *succini* means "from amber."

Discussion

The wing venation, 5-segmented antenna, shape of the rhinaria and the general habitus suggests that the fossil species belongs in the family Hormaphididae. The presence of distinctly visible mesothoracic lobes is, however, not typical of Hormaphi-

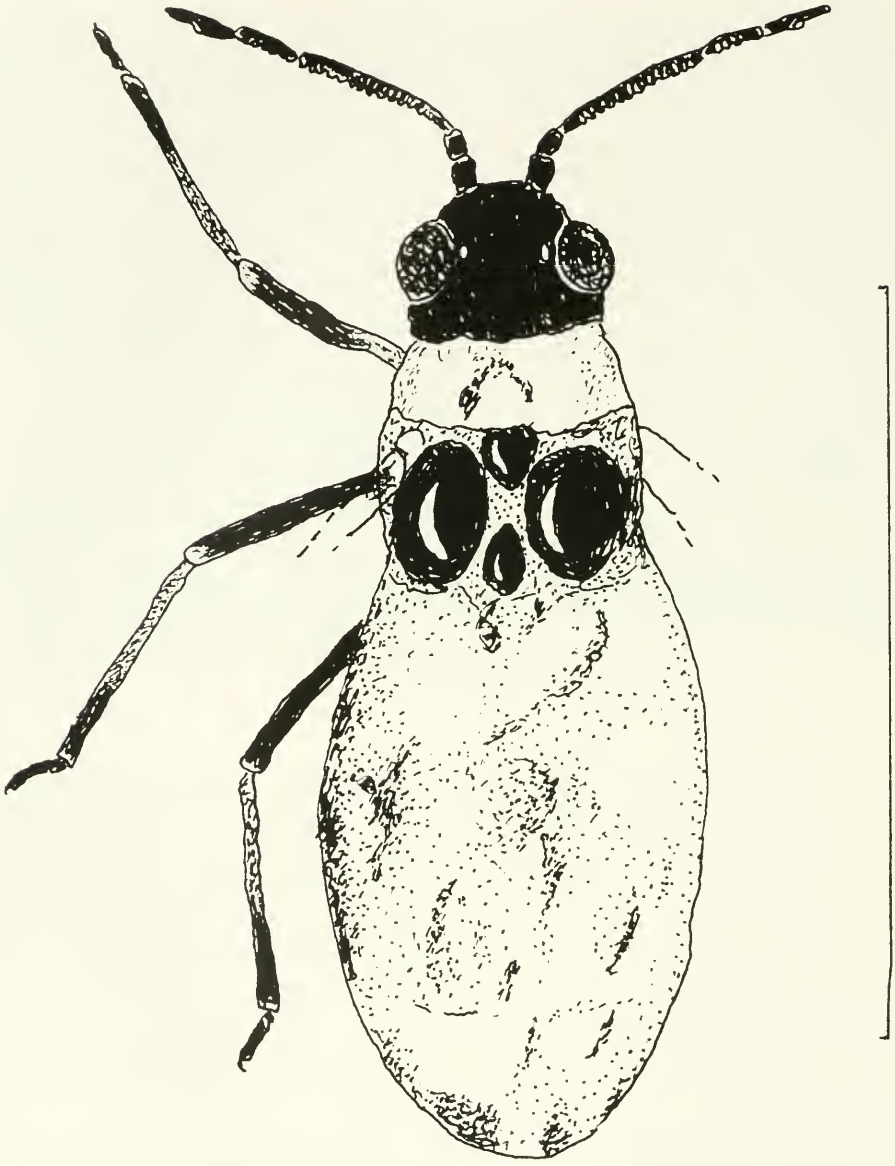

Fig. 2. Dorsal view of body of *Dominicaphis succini* (scale = 1 mm).

didae. The pattern in this family is a rather flat mesothorax with the wings flat in repose. Usually distinctly visible mesothoracic lobes indicate that the wings are held roof-like in repose. In this respect *D. succini* differs from all known species of Hormaphididae. Dr. Aoki kindly sent us a slide with an alate viviparous female of *Aleurodaphis blumeae* van der Goot and stated that Moritsu (1983: 200) reported that alatae of this latter species keep their wings roof-like in repose. However Moritsu (1983) also shows two color photos of *A. blumeae* (see page 14), in which the wings clearly are flat in repose. The mesothorax of *A. blumeae* shows sutures separating the lobes, however less distinctly than in the fossil. The two species are similar in some

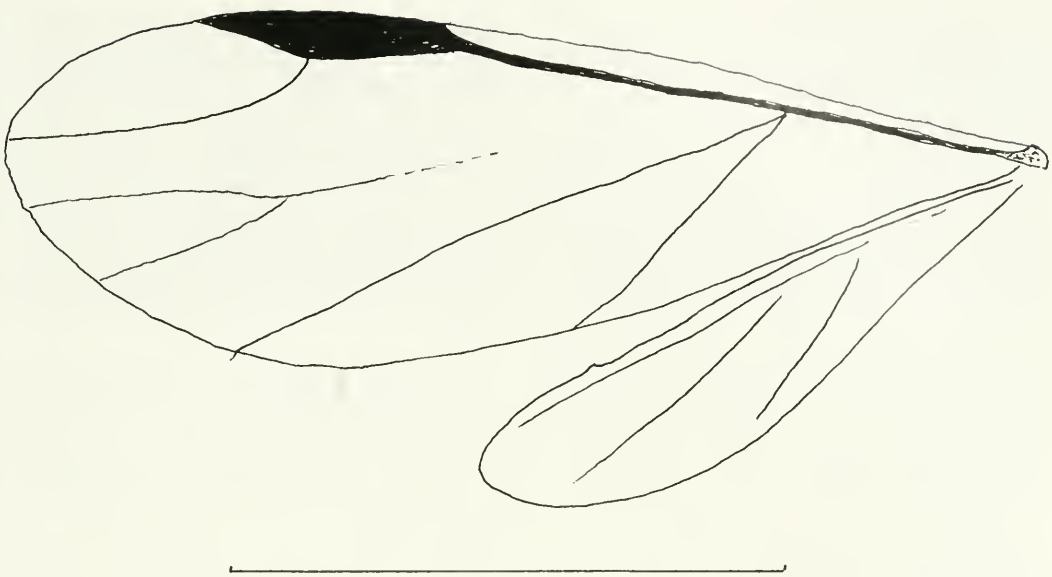

Fig. 3. Wings of *Dominicaphis succini* (scale = 1 mm).

features such as wing venation, body length and length of antennae. In addition, antennal segment III is 2.1 times as long as segment IV in *D. succini* and 1.7–3.0 in *A. blumeae*, 1.7 times as long as segment V in the former and 1.4–2.2 in the latter, and the number of secondary rhinaria in *D. succini* lies within the range of those in *H. blumeae* which are; segment III with 11–17, IV with 4–6 and V with 1–7 (Noordam 1991). However *A. blumeae* has a knobbed cauda while *D. succini* has a rounded cauda and the siphuncular pores of *A. blumeae* are surrounded by dark sclerites, which apparently are absent from *D. succini*, so the two species are probably not closely related.

The pointed projection below the posterior end of the abdomen in *D. succini* is a structure unknown in Hormaphididae and in all other families within the extant Aphidoidea. It resembles an ovipositor, but this is strange since representatives of the superfamily Aphidoidea with oviparous parthenogenetic females have not been found later than the Cretaceous, and the fossil specimen definitely belongs to an extant family of the Aphidoidea.

Previously, *Aleurodaphis* had been considered as belonging to the tribe Cerataphidini, but Stern (1994: 206) stated: "Surprisingly, *Aleurodaphis blumeae*, which has been placed in the Cerataphidini, based on morphological evidence, appears distantly related to the other cerataphidines, and may represent a lineage basal to all remaining Hormaphididae." Stern's phylogenetic tree was based on DNA spanning the mitochondrial cytochrome oxidase I and II genes, and he used the eriosomatid species *Pemphigus microsetosus* as the outgroup. The fossil species may have split off from the base of the hormaphidid lineage before the character "wings flat in repose" evolved, perhaps close to the point where the eriosomatid and the hormaphidid lineages separated.

The fossil is the first alate specimen of a Hormaphididae described from the mid-Tertiary, although an apterous specimen of another species. *Electrocornia antiqua* Heie, was described from Baltic amber (Heie 1972). The family must have originated somewhat earlier, probably close to the Cretaceous-Tertiary boundary since rep-

resentatives of the sister group, the family Eriosomatidae, occur in large numbers in Baltic amber (Heie, 1985).

Especially in the structure of the mesothorax, the fossil also resembles extant genera of the family Eriosomatidae (formerly known as Pemphigidae), especially *Eriosoma* Leach (Eriosomatinae: Eriosomatini). However, *D. succini* differs from this genus in the following aspects: cubitus branches in the fore wing are not separated at the point where they depart from the main vein, the antenna consists of five segments, all carrying rhinaria, and antennal segment III is shorter than segments IV + V. The fossil differs from *Kaltenbachiella* Schouteden in the presence of a media fork, and it differs from *Colopha* Monell by possessing two oblique veins in the hind wing. All eriosomatine alatae have six antennal segments except at least one, *Colophina clematicola* (Shinji), which has 5-segmented antennae. As the other species of the genus *Colophina* Börner have alatae with 6-segmented antennae, it is likely that *C. clematicola* has only recently acquired the 5-segmented antennae, so this similarity to *Dominicaphis succini* is no proof of a close relationship. Dr. Aoki most kindly loaned us a specimen *C. clematicola*, and it differs from the fossil in having broader ring-shaped rhinaria, a shorter antennal segment IV and a shorter distance between the bases of the cubitus branches.

Biology

It is impossible to determine the host plant of *Dominicaphis succini*, but it is reasonable to assume that it was a woody angiosperm since most extant members of the Hormaphididae feed on these plants. The amber-producing tree, *Hymenaea protera* Poinar (1991) need not be the host plant since the fossil is alate and could have flown or been blown into the resin.

Some species of Hormaphididae alternate between two woody hosts (I: *Styrax, Distylum* a.o., II: *Betula, Quercus* a.o.) and have a two-year-cycle, while others are monophagous. Some extant members feed on monocots, including bamboo. Fossil remains of bamboo have been found in Dominican amber (Poinar and Columbus 1992; Poinar and Poinar 1999) and could have been the host plant of *D. succini*. *Aleurodaphis blumeae* is monophagous on *Blumea*, which belongs to the Asteraceae, a group which has not been reported from Dominican amber (Poinar and Poinar 1999).

Most extant species of the Eriosomatini have host alternation between *Ulmus* and either roots of *Ribes* or herbaceous plants but neither of these genera have been reported from Dominican amber (Poinar and Poinar 1999).

The Hormaphididae, contrary to aphids in general, including the Eriosomatidae, is mainly a tropical family with most species in eastern and southeastern Asia, but also several in America.

Acknowledgments

The authors thank Dr. S. Aoki for taxonomic comments and loaning slides of *Colophina clematicola* and *Aleurodaphis blumeae* and Dr. R. L. Blackman for informing us about the photographs of *A. blumeae* in Moritsu (1983).

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THE FIRST FOSSIL OF A PLEASING LACEWING (NEUROPTERA: DILARIDAE)

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Abstract.—The first fossil pleasing lacewing (Dilaridae) is described and figured from a single male preserved in Eocene Baltic amber. The individual represents a new genus and species of Dilarinae, ***Cascadilar eocenicus***. The genus can be distinguished from other members of the Dilarinae most notably by the double pectination of the third antennal segment, the relatively well-developed mouthparts, the absence of nygmata, and the slightly narrower hind wing relative to the forewing.

Key Words: Baltic amber, *Cascadilar,* Dilarinae, Eocene, paleontology, Planipennia

The pleasing lacewings comprise a small family (Dilaridae) of uncommon neuropterous insects with 67 described species distributed in Asia (Nakahara 1963, Hynd 1992), Africa (Minter 1986), Europe (Aspöck et al. 1980), and the Americas (Adams 1970, Penny 1981, 1994). The family can be readily recognized by the pectinate antennae of males, the exserted ovipositor of females, and the presence of three prominent tubercles on the vertex (Aspöck et al. 1980, New 1989, Oswald 1998). Species of the family are typically quite small (forewing lengths range from 3–22 mm) and frequently occur around dead wood where it is believed they oviposit in the crevices of, or just under the surface of, bark. The Dilaridae has been placed as the sister group to a Mantispidae + Berothidae + Rhachiberothidae clade based on the shared presence of a relatively flat larval head and the band-like, broadly inserting cardo+stipes (Aspöck 1992). The family was hypothesized by Schlüter (1986) to have arisen in the Upper Jurassic, even in the absence of any dilarid fossils. This age was based on the presumed phylogenetic affinity of the family with the Mantispidae and Berothidae (at that time inclusive of the Rhachiberothidae), the latter of which was represented among the Lower Cretaceous fauna by two genera (Whalley 1980). By any account, the geological range of the Dilaridae can now be extended back to the Middle Eocene on the basis of the fossil reported herein.

The neuropteroid fauna of the Baltic amber has been investigated by a number of authors—Megaloptera (Pictet 1854, Weidner 1958, Wichard 1997), Raphidioptera (Carpenter 1956, Engel 1995, Hagen 1854), Planipennia (Hagen 1854, Keilbach 1982, Krüger 1923, MacLeod 1970, Meinander 1972, 1975, Parfin and Gurney 1956, Pictet and Hagen 1856). This is presently the best known amber for Neuropteroidea with only a few specimens reported from British, Dominican, French, Lebanese, and Mexican ambers.

The few measurements presented in the descriptions are approximate since the optimal angle for taking a given measure was difficult due to the surface of the amber.

Fig. 1. Photomicrograph of male holotype of *Cascadilar eocenicus*.

SYSTEMATIC PALEONTOLOGY

Cascadilar Engel, new genus

Type species.—*Cascadilar eocenicus* Engel, new species.

Description.—Vertex with three prominent tubercles, covered with minute setae. Antenna pectinate (Figs. 1–2); elongate lateral processes on distal halves of antennal segments three through eight; antennal segment three with two lateral processes, basal process short, distal process elongate; basal two segments and distal four segments without lateral processes (Fig. 2). Short scythe-like mandibles protruding from face; maxillary palpus extending just beyond apices of mandibles, apparently five-segmented (difficult to see all segments); labial palpus minute, not reaching beyond borders of head in any direction (number of segments indeterminate from the fossil). Wings strongly pubescent; MA fusing in forewing with radial system near wing base, separating from radial system well before separation of R1 and Rs (Fig. 3); nygmata absent; trichosors well-developed, shorter along anterior wing margin and absent basally on anterior margin; hind wing slightly narrower than forewing.

Etymology.—The generic name is a combination of the Latin word *cascus* (meaning "old") and *Dilar* (type genus of the family). The gender is masculine.

Comments.—*Cascadilar* is a member of the subfamily Dilarinae as evidenced by the branching of MA prior to the separation of R1 and Rs in the forewing and by the pos-

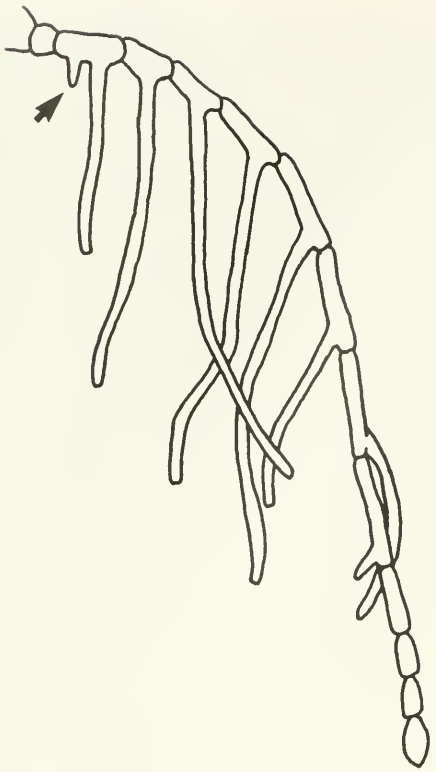

Fig. 2. Right male antenna of *Cascadilar eocenicus*, as preserved. Arrow indicates short basal process of antennal segment three.

session of more than three distal antennomeres without lateral processes. It can be most notably distinguished from other dilarine genera by the presence of two lateral processes on the third antennomere, the relatively well-developed mouthparts (a primitive feature among the family), and the absence of nygmata in the forewing.

Cascadilar eocenicus Engel, new species
(Figs. 1–3)

Diagnosis.—As for the genus.

Description.—*Male:* Total body length 2 mm (excluding antennae). Forewing length 3.7 mm. Hind wing length 3.4 mm. Head transverse, wider than long. Antenna 14-segmented; long, extending posteriorly approximately three-quarters of distance to abdominal apex; scape roughly quadrate; distal, non-pectinate segments progressively shorter than segments with lateral processes; distal-most segment pointed at apex (Fig. 2). Eyes large, spherical. Pubescence of head exceedingly sparse and short. Integument of head apparently brown, slightly darker on vertex surrounding tubercles.

Pronotum slightly wider than long, with scattered fuscous pubescence; pubescence sparse except laterally where it is longest and relatively numerous; remainder of thorax with almost no pubescence; thorax brown. Legs slender, with scattered minute, silvery setae; tibial spurs absent; tarsi five-segmented; first segment about as long as combined lengths of second, third, and fourth segments; second segment about as long as fifth; third and fourth segments progressively shorter than second segment; claws minute. Forewing relatively broad, densely pubescent, particularly between Sc and anterior margin and on basal third; 13 crossveins in costal margin; no sc crossveins; three crossveins between R1 and Rs; Rs five-branched; other details of forewing venation depicted in Fig. 3. Wing membrane hyaline, without fuscous patterning; veins amber; pubescence slightly fuscous.

Abdomen apparently without pubescence, integument shining and appearing faintly imbricate; apparently uniformly brown. Most of terminalia not visible in fossil except eighth and ninth terga appear unmodified without emargination or processes along borders; ectoproct with long, fuscous setae, progressively becoming shorter towards apex; apex dark brown and conspicuous.

Female: Unknown.

Holotype.—Male, Eocene Baltic amber, deposited in the California Academy of Sciences (formerly in P. Craig collection), San Francisco. The specimen bears three labels which read as follows: Baltic Amber, Pat Craig Collection, February 1996/Holotype, *Cascadilar eocenicus* Engel, desig. M. S. Engel/Baltic amber, Diptera, Mycetophilidae, fungus gnat (2).

Preservation.—The specimen is wonderfully preserved lacking the mold found on

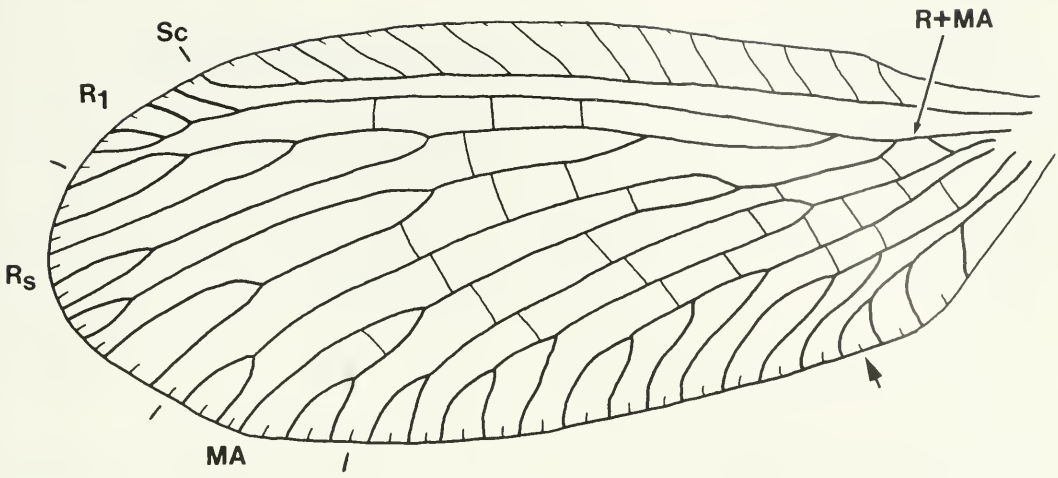

Fig. 3. Left forewing venation of *Cascadilar eocenicus* with major vein systems discussed in the text indicated. Large arrow indicates one of the trichosors present along the posterior margin. Wing hairs omitted.

many Baltic amber inclusions. Two mycetophilid flies (Fig. 1) unfortunately obscure some portions of the lacewing.

Etymology.—The specific epithet is derived from the epoch name, Eocene.

Acknowledgments

I owe great thanks to Pat Craig for allowing me to study and describe this fine fossil from his collection and for permitting its deposition in the collection of the California Academy of Sciences, San Francisco. My work at the American Museum of Natural History is supported by Robert G. Goelet, Chairman Emeritus of the Board of Trustees of the American Museum of Natural History, and by Jerome G. Rozen, Jr. The manuscript was improved by comments from David R. Smith and two anonymous reviewers to whom I extend my appreciation.

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REDESCRIPTION OF *SAVA* AMYOT AND SERVILLE 1848 (HETEROPTERA: REDUVIIDAE: HARPACTORINAE)

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Abstract.—*Sava*, an exclusively Neotropical genus, and its only included species, *S. tuberculata* (Gray), are redescribed. The species is known from Guyana and French Guiana.

Key Words: Heteroptera, *Sava, Sava tuberculata*, Reduviidae, Neotropical, Guyana, French Guiana

The Neotropical genus *Sava*, proposed by Amyot and Serville (1843) for their new species *S. coronata* from Cayenne, was cataloged as a valid genus by Stål (1872), Wygodzinsky (1949), and Maldonado (1990). Stål (1872) assigned *Reduvius tuberculatus* Gray (1832), also described from Cayenne, to *Sava* and made *S. coronata* a junior synonym of it.

The single species of this genus is characterized by a peculiar inflated pronotum that extends over the basal two-thirds of the abdomen. According to Elkins (1969), the wasp mimetic genera *Coilopus* Elkins and *Notocyrtus* Burmeister possess comparably enlarged pronota, but these are not closely related to *Sava*.

The present contribution is to redescribe the genus *Sava* and its only included species.

MATERIALS AND METHODS

This study is based on material provided by the following institutions: The Natural History Museum, London, U.K. (BMNH) and Instituto de Biología de la Universidad Autónoma de México, México, D.F., México (UNAM).

The terminology used for the external morphology follows Maldonado and Carpintero (1993). The measurements (expressed in millimeters) and ratios are according to Coscarón (1994a). For this revision, a total of four measurements and 11 ratios were selected. The terminology employed for the characters of the female genitalia is detailed in Coscarón (1994b).

SYSTEMATICS

Sava Amyot and Serville

Sava Amyot and Serville 1843: 379; Wygodzinsky 1949: 46; Maldonado 1990: 293.

Type species.—*Sava coronata* Amyot and Serville, by monotypy.

Redescription.—*Head* (Fig. 2): Slightly less than half as long as pronotum; narrowing posteriorly behind eyes into a long neck; subantennal spines absent; genae without spine; eyes not surpassing upper and lower margins of head; interocular suture straight; second rostral segment more than double length of first rostral segment;

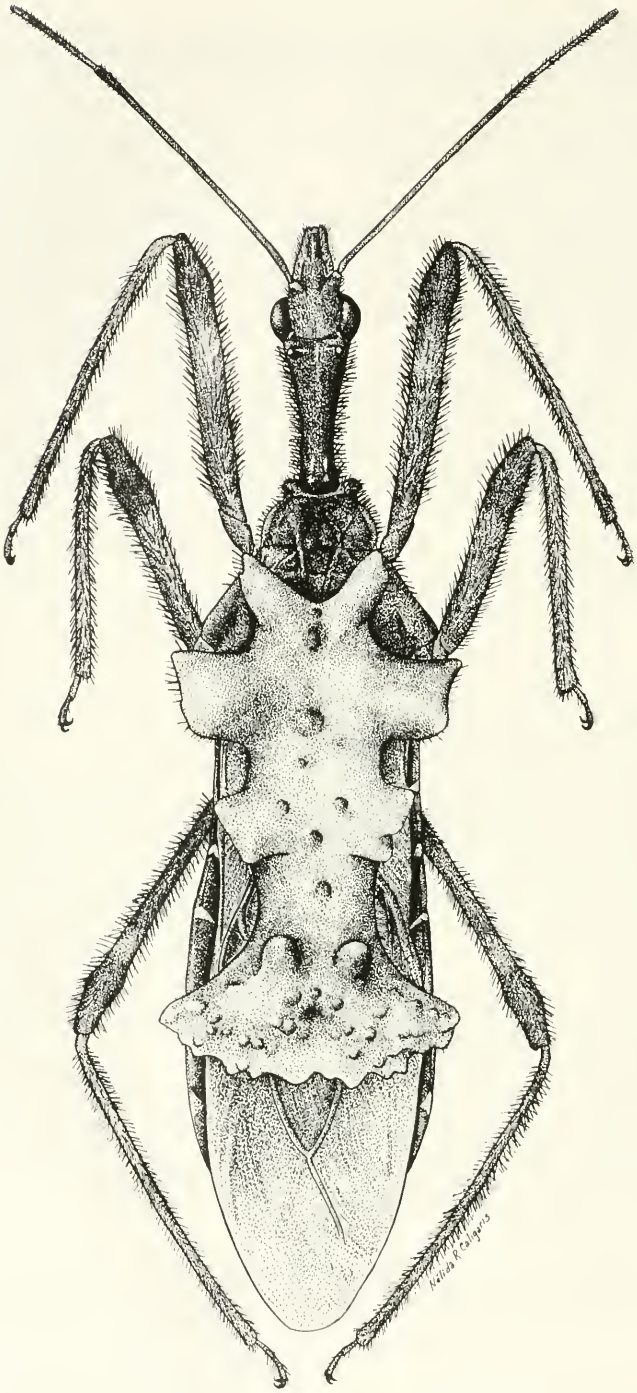
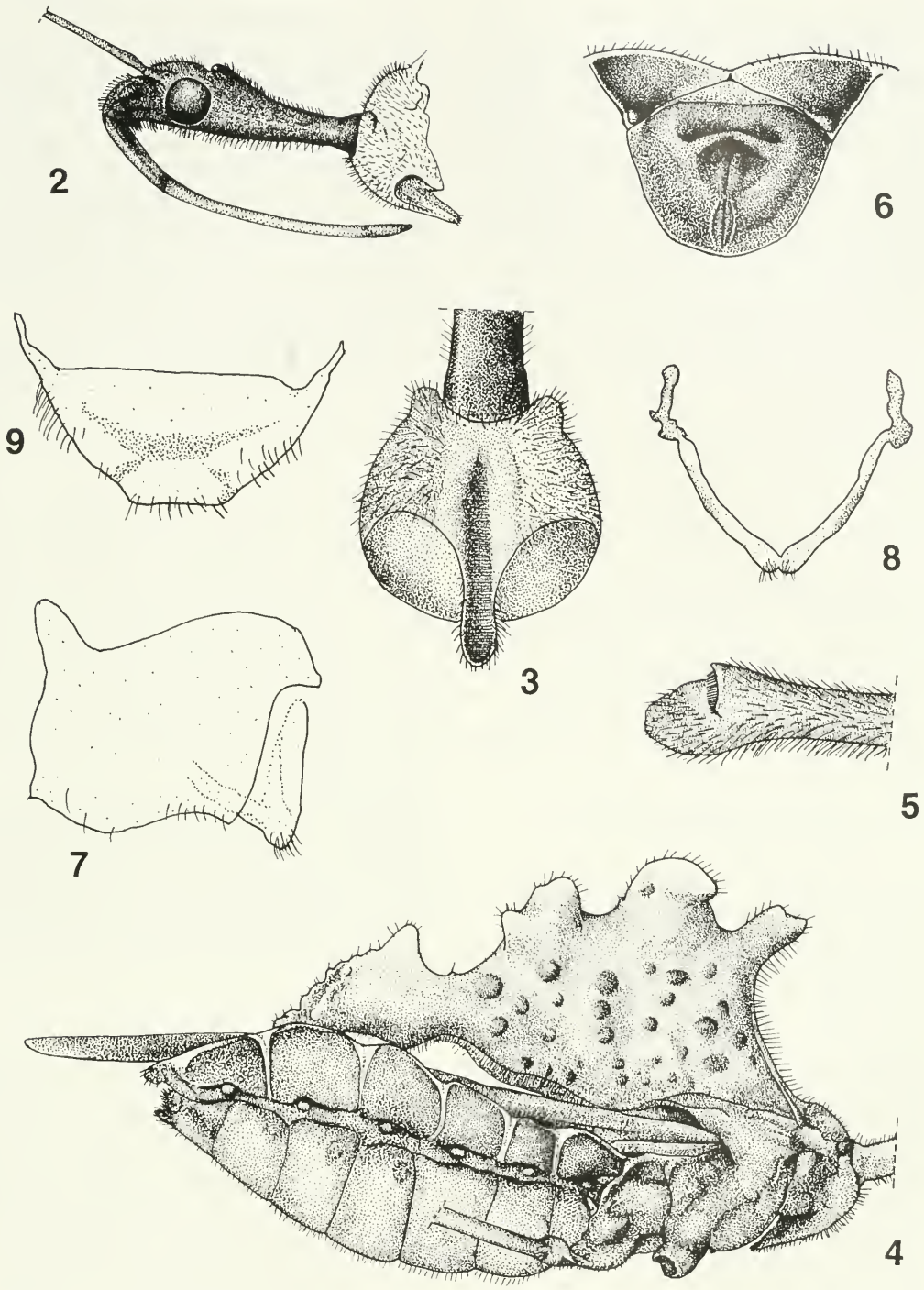


Fig. 1. *Sava tuberculata*, dorsal view of female.



Figs. 2–9. *Sava tuberculata*. 2, Head, lateral view. 3, Stridulatory sulci. 4, Pronotum, scutellum, and abdomen, lateral view. 5, Fore tibia, distal portion. 6, Female genitalia, caudal view. 7, Gonocoxite and gonapophysis VIII. 8, Gonocoxite IX. 9, Tergites IX, X.

antenna long and slender. *Pronotum* (Fig. 5): Longer than wide, subpentagonal; anterior lobe lacking spines; longitudinal sulcus faint anteriorly, deeply grooved posteriorly and reaching posterior lobe; anterolateral angles not protruding; hemelytra (Fig. 5) covered by pronotum on basal 2/3, pronotum not passing apex of abdomen, hemelytra extending well beyond apex of abdomen; upper surface of pronotal lobes sculptured, multileveled (Fig. 4). *Legs:* Lacking spines, moderately long, hind femur reaching beyond abdominal segment IV; apices of femora with 1 + 1 short blunt lateral projections, forefemur in dorsal view slightly incurved, postbasally incrassinate, gradually narrowing to apex; foretibia curved with small preapical spur (Fig. 7) and small apical pad of setae, tibia and femur beneath with dense short pubescence. *Abdomen* (Fig. 5): Elongate, narrow basally, gradually widening to apex of fourth segment; fifth and sixth segments more or less abruptly and conjointly foliaceus.

Distribution.—Neotropical: Guyana, French Guiana.

Sava tuberculata (Gray)
(Figs. 1–9)

Reduvius tuberculatus Gray 1832: 244.
Sava coronata Amyot and Serville 1843: 379; Stål 1872: 92 (synonymy).
Sava tuberculata: Stål 1872: 92; Wygodzinsky 1949: 46; Maldonado 1990: 293.

Redescription.—Female: *Head* (Fig. 2): Dark brown, setae dark brown, granulations and rugosities scattered throughout surface; eyes not reniform; ocelli on tubercles; antenna brown, second segment densely pilose; rostrum brown. *Pronotum:* Anterior lobe dark brown with short setae, granulated and without rugosities and without setae along edges. Posterior lobe basally same color as anterior lobe, with short setae and strongly sculptured (Fig. 4); projection pale brown, with short setae and sparse conspicuous granulations. *Scutellum* (Fig. 4): Covered by pronotum. Pleura dark brown with pilosity; stridulatory sulcus pale brown; sterna dark brown with short setae. *Legs:* Brown with femora darker, brown in macropterous form. *Hemelytron:* Pale brown, with few short setae laterally. *Abdomen:* Connexivum visible in dorsal view, dark brown with joint between connexival segments pale brown; stigma pale; urosternites dark brown except segments just before genitalia, paler medially; median area with short setae. Genitalia as in Figs. 6–9.

Measurements and ratios: Total length, 19.2; width pronotum, 3.84; width abdomen, 4.86; head length/head height, 3.76; length anteocular region/length postocular region, 0.41; eye length/eye width, 2.12; eye height, 0.71; length eye interocular region/ocellar diameter, 6.12. Antennal segments length relationships: segment 1/segment 2, 3.25; segment 1/segment 3, 0.91; segment 1/segment 4, missing. Rostral segments length relationships: segment 1/segment 2, 0.44; segment 1/segment 3, 2.03. Pronotum length, 14.08; length of pronotal anterior lobe/pronotal posterior lobe, 0.90.

Male: Unknown.

Distribution.—Guyana, French Guiana.

Material examined.—Holotype female: Cayenne, *R. tuberculatus* Gray, located in BMNH although Elkins (1969) considered it lost. Additional material: 1 female, Guyana, Mabaruma, Power Line Road, 17-IV-1994 (UNAM).

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REVIEW OF THE EASTERN NORTH AMERICAN *DICYPHUS*, WITH A KEY TO SPECIES AND REDESCRIPTION AND NEOTYPE DESIGNATION FOR *D. VESTITUS* UHLER (HETEROPTERA: MIRIDAE)

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Abstract.—*Dicyphus vestitus* Uhler is redescribed and a neotype from Colorado is designated for it. A dorsal adult habitus and selected scanning electron micrographs of *D. vestitus* and an identification key are provided to help recognize the eastern North American species of the genus. Distributions and host records are given for other eastern North American species.

Key Words: Insecta, Heteroptera, Miridae, plant bugs, eastern North America, *Dicyphus*, redescription, neotype, distribution, hosts, key

In a continuing effort to clarify and describe the mirid fauna of eastern North America, I redescribe the poorly known species *Dicyphus vestitus* Uhler and designate a neotype to ensure stability. Henry and Wheeler (1988) listed 25 species of *Dicyphus* Fieber for Canada and the United States, eight of which are recorded from east of the 95th Meridian. Cassis (1986), in a comprehensive treatment of the Dicyphinae, showed that more than half the species previously placed in *Dicyphus* belonged in other genera, an interpretation followed by Schuh (1995) in his catalog of the Miridae of the world.

The subfamily placement of *Dicyphus* and related genera is unsettled. Cassis (1986) placed these taxa in Dicyphinae, whereas Henry and Wheeler (1988) grouped them as the tribe Dicyphini, within Bryocorinae. Schuh (1995) followed his earlier treatment (Schuh 1976) by reducing the group to the subtribe Dicyphina, within a redefined Dicyphini (which also included the subtribes Monaloniina and Odoniellina), all within Bryocorinae, a problematic subfamily that almost certainly is not monophyletic.

The genus *Dicyphus* in eastern North America is comprised of *D. vestitus*, along with *D. discrepans* Knight, *D. famelicus* (Uhler), *D. gracilentus* Parshley, and *D. hesperus* Knight. The remaining three eastern U.S. species of *Dicyphus* listed by Henry and Wheeler (1988) belong in *Tupiocoris* China and Carvalho [*T. rhododendri* (Dolling), *T. rubi* (Knight), and *T. similis* (Kelton)] (Schuh 1995).

In this paper, I redescribe *D. vestitus*, designate a neotype from Colorado, provide new distribution records, and give the first host association for this species. An adult dorsal habitus and SEM micrographs of *D. vestitus* and an identification key are provided to help recognize the eastern North American species of *Dicyphus*. Distributions and hosts are also summarized for the other eastern North American species.

Dicyphus discrepans Knight

Dicyphus discrepans Knight 1923: 477; Henry and Wheeler 1988: 262; Schuh 1995: 489.

Dicyphus discrepans was described from New York (Knight 1923) and later recorded from Alberta, British Columbia, Indiana, Michigan, Minnesota, New Brunswick, New Hampshire, North Dakota, Ontario, Oregon, Quebec, Saskatchewan, Washington, and Wisconsin (Henry and Wheeler 1988). *Aster* sp. [Asteraceae] is reported as the host (Knight 1923).

Dicyphus famelicus (Uhler)

Idolocoris famelicus Uhler 1878: 413.
Dicyphus famelicus: Atkinson 1890: 128; Henry and Wheeler, 1988: 262; Schuh 1995: 490.

Dicyphus famelicus was described from New Hampshire (Uhler 1878) and later reported from Illinois, Indiana, Maine, Massachusetts, Michigan, New Brunswick, New Jersey, New York, North Carolina, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, West Virginia, and Wisconsin (Henry and Wheeler 1988). New state records are Maryland, Minnesota, and Virginia. The host is *Rubus odoratus* L. [Rosaceae] (Knight 1923) and *Rubus* sp.

Uhler's (1878) description was based on a male in the T. W. Harris Collection. I have studied the holotype deposited in the MCZ collection [Type number 26449, drawer 41], and find that it agrees in all respects with the currently accepted concept of *D. famelicus*. The type, glued to a paper triangle, is in good condition, except that segments III and IV on both antennae are missing. The exact label data are as follows: label 1, "101, N. H." [also present on this label is a faded "u," written in red ink]; 2, "97"; 3 (red label), "M.C.Z. Type 26449."

Other specimens examined.—MARYLAND: 8 ♂, 6 ♀, Garrett Co., Deep Creek Lake, 5 June 1982, T. J. Henry, taken on *Rubus* sp. (USNM). MINNESOTA: 2 ♂, 1 ♀, Brainerd, Aug. 23–25, 1971, H. H. Knight (USNM). NORTH CAROLINA: 1 ♀, McDowell Co., nr. Little Switzerland, Rt. 226A, 10 Jul. 1988, T. J. Henry and A. G. Wheeler, Jr., on *Rubus* sp. nr. *odoratus* (USNM). VIRGINIA: 3 ♂, 4 ♀, Jefferson National Forest, June 6, 1967, R. C. Froeschner (USNM); 3 ♀, Bath Co., Rt. 678, 4 mi. N. Williamsville, 10 June 1984, T. J. Henry and A. G. Wheeler, Jr., on *Rubus* sp. (USNM); 2 ♂, 2 ♀, Highland Co., Rt. 250, Head Waters (shale barren), 9 June 1984, T. J. Henry and A. G. Wheeler, Jr., on *Rubus* sp. (USNM).

Dicyphus gracilentus Parshley

Dicyphus gracilentus Parshley 1923: 21; Henry and Wheeler 1988: 263; Schuh 1995: 491.

Dicyphus gracilentus was described from Illinois (Parshley 1923) and later recorded from Indiana and Ohio (Henry and Wheeler 1988). The host is leafcup, *Polymnia canadensis* L. [Asteraceae] (Parshley 1923).

Dicyphus hesperus Knight

Dicyphus hesperus Knight 1943: 56; Henry and Wheeler 1988: 263; Schuh 1995: 492.

Dicyphus hesperus is reported from Alberta, British Columbia, California, Colorado, Idaho (holotype), Illinois, Manitoba, Michigan, Minnesota, Montana, Nevada, New Brunswick, North Dakota, Ontario, Oregon, Quebec, Saskatchewan, Utah, and Washington (Kelton 1980, Henry and Wheeler 1988). Hosts recorded in the original description (Knight 1943) are mullein, *Verbascum* sp., *Verbascum virgatum* Stokes [Scrophulariaceae], *Stachys albens* Gray [Lamiaceae], and tomato [Solanaceae]. Field mint, *Mentha arvensis* L. [Lamiaceae], also has been given as a host (Kelton 1980).

Dicyphus vestitus Uhler
(Figs. 1–5)

Dicyphus vestitus Uhler 1895: 46; Henry and Wheeler 1988: 264; Schuh 1995: 495.

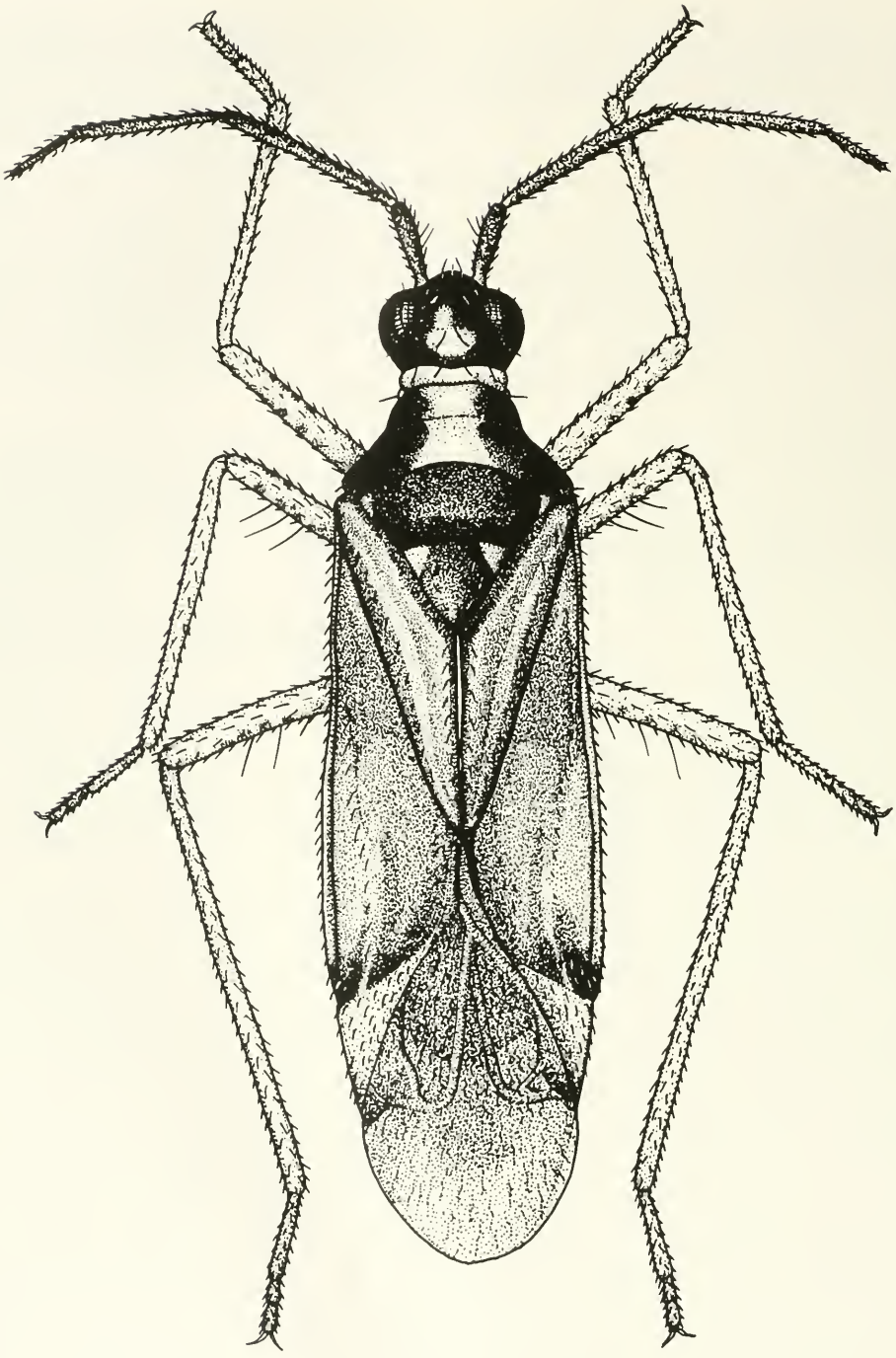
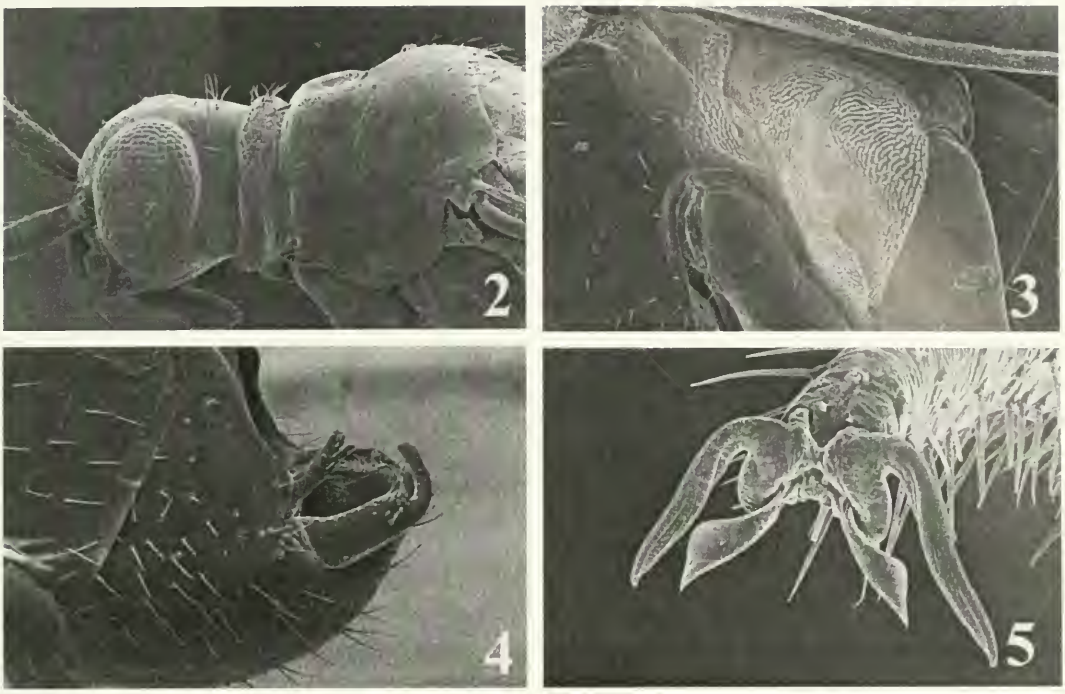


Fig. 1. Dorsal adult habitus of *Dicphyus vestitus* (♂).



Figs. 2–5. *Dicyphus vestitus*. 2, Head and pronotum, lateral aspect (110×). 3, Ostiolar area (256×). 4, Male genital capsule, lateral aspect (266×). 5, Claw (740×).

Dicyphus notatus Parshley 1922: 16. Synonymized by Knight 1927: 104.

Diagnosis.—*Dicyphus vestitus* is best recognized by the dark antennal segment II; pale legs; the coloration of the pronotum, ranging from broadly pale dorsally with only the lateral margins fuscous or black to predominately black with only the median area pale; and by the tubercle on the genital capsule just above the base of the left paramere.

Description.—*Male* (n = 10): Length 3.32–3.68 mm, width 1.00–1.06 mm. *Head* (Fig. 2): Width 0.54–0.56 mm, vertex 0.20–0.22 mm. *Rostrum:* Length 1.36–1.42 mm, extending beyond metacoxae to about 3rd abdominal segment. *Antenna:* Segment I, length 0.30–0.32 mm; II, 0.66–0.74 mm; III, 0.54–0.60 mm; IV, 0.34–0.36 mm. *Pronotum:* Length 0.40–0.42 mm, basal width 0.76–0.82 mm. *Genitalia:* Genital capsule rounded (Fig. 4) , with a short slender tubercle on left side above paramere; left paramere elongate, slender, narrowed and curved apically (Fig. 4); right paramere greatly reduced, wedgeshaped, tapered apically; vesica simple, membranous.

Female (n = 10): Length 3.44–3.64 mm, width 0.96–1.04 mm. *Head:* Width 0.56–0.58 mm, vertex 0.20–0.22 mm. *Rostrum:* Length 1.36–1.40 mm. *Antenna:* Segment I, length 0.30–0.32 mm; II, 0.74–0.78 mm; III, 0.56–0.58 mm; IV, 0.30–0.34 mm. *Pronotum:* Length 0.40–0.42 mm, basal width 0.82–0.84 mm.

General coloration shiny fuscous on head and pronotum, with paler gray to brown areas accented with dark brown on hemelytra. Head (Fig. 2) shiny fuscous, with a pale transverse oval spot just behind and between eyes. Rostrum pale brown, with segment IV becoming dark brown on apical half. Antenna usually uniformly fuscous, but with segment I sometimes slightly paler or reddish brown toward basal half. Pronotum trapeziform, strongly narrowed from base to anterior margin, basal margin deeply sinuate; coloration variable, ranging from

predominately pale dorsally with only the lateral margins shiny fuscous to largely fuscous or black with the area between the calli and midline of disc pale, collar pale or whitish, narrow transverse suture immediately behind collar tinged orange red; calli well delimited, separated from collar and disc by a distinct transverse suture anteriorly and posteriorly; mesoscutum broad, uniformly dull fuscous, anterior angles sometimes pale yellowish brown; scutellum dull fuscous, with anterior angles pale yellowish. Hemelytra generally pale smoky brown to gray, margins of clavus, including commissure, and apex of corium and cuneus darker brown; membrane and veins brown, slightly paler just beyond apex of cuneus. Ostiolar area (Fig. 3) grayish or brown, tinged with pale orange, particularly median area of auricle. Ventral surface shiny brown to fuscous; thoracic segments more fuscous, abdomen more dark yellowish brown. Legs uniformly pale yellowish brown, except for bases of coxae, distal (3rd) tarsomeres, and claws slightly darker brown; claws deeply dentate at bases (Fig. 5).

Remarks.—The coloration of this species is quite variable. The adult habitus furnished in this paper (Fig. 1) is based on the much darker specimens from Virginia that have the pronotum predominately fuscous to black, with only a narrow pale area between the calli and median line of the disc, as well as more darkly marked hemelytra, particularly the apex of the corium and cuneus. Most northern and western specimens of this species have much of the dorsum of the pronotum broadly pale, with only the pleural areas darkened, and the hemelytra have less distinct dark areas at the apex of the corium and cuneus. However, the general size, lengths of the antennal segments and their proportions to other body structures, shape of the left paramere, and presence of a tubercle above the left paramere convince me that these populations represent a single species.

Host.—The only previous plant association was Froeschner's (1949: 162) report of this species hibernating under leaves of mullein, *Verbascum* sp. [Scrophulariaceae], in Missouri. Based on collections by A. G. Wheeler, Jr, this species is now known from heart-leaved skullcap, *Scutellaria ovata* J. Hill [Lamiaceae], a plant frequenting shale barrens and other dry shale outcrops, mostly on the eastern slopes of the Alleghenies (Strausbaugh and Core 1978, Wheeler 1995).

Distribution.—This species was described from Colorado (Uhler 1895) and later reported from California, Idaho, Illinois, Iowa, Minnesota, Missouri, New Hampshire, New Mexico, New York, Ohio, and South Dakota (Wheeler and Henry 1988). Records from California, New Mexico and, perhaps, other western records need confirmation. Virginia represents a new state record and a considerable range extension in the eastern United States.

Type designation.—Uhler (1895) stated in his original description that the types of this species were from Fort Collins, Colorado, collected from May 20th to June 4th and from Montrose on June 24th. Only one male Baker specimen from Fort Collins fitting the original description was discovered in the USNM collection, but it was taken on June 7th and, therefore, could not have been part of the original series. This specimen fits the original description and the accepted concept followed by Knight (1927, 1929), including the presence of a distinct tubercle above the left paramere, and is here designated as the neotype: Label 1, "Colo 1547" [Fort Collins, 6-7-95]; 2, "Collection CF Baker"; 3, "Dicyphus vestitus Uhler, det RI Sailer"; 4, "Neotype: ♂, Dicyphus vestitus Uhler, by T. J. Henry." Deposited in USNM collection.

Other specimens examined.—COLORADO:1 ♀, Ft. Collins, Col., 5/24, 99, H. H. Knight collection, 1976 (USNM); 1 ♀, Ft. Collins, Dixon's Canyon, Aug. 19, 1898, E. D. Ball (USNM). ILLINOIS: 1 ♂, Urbana, III-18-1888; (USNM); 1 ♂, Cary, May 14, 1936, Ross & Mohr (USNM).

IOWA: 17 ♂, 16 ♀, Ames, May 7, 1927, H. H. Knight (USNM). MINNESOTA: 1 ♀, Norman Co., ix-30-1932, A. A. Nichol (USNM). MISSOURI: 1 ♂, Midway, III-25-1939, R. C. Froeschner (USNM). NORTH DAKOTA: 1 ♂, 1 ♀, Fargo, Oct. 16 1921, O. A. Stevens (USNM). VIRGINIA: 30 ♂, 35 ♀, Alleghany Co., Rte. 42 NE of Clifton Forge, 1 August 1993, A. G. Wheeler, Jr., on *Scutellaria ovata* (USNM); 3 ♂, 11 ♀, Bath Co., Millboro Barrens, 17 July 1993, A. G. Wheeler, Jr., on *Scutellaria ovata* (USNM; 3 ♂, 7 ♀, and nymphs (all in alcohol), Rockbridge Co., James River Face Wilderness, 0.9 mi. ENE of Sulphur Spring, el. 2,260′, 1 Sept. 1993, T. J. Rawinski, collected on *Scutellaria ovata* (USNM).

Key to the Eastern North American Species of *Dicyphus*

1. Pronotum black, at least along lateral margins or pleural areas; antennal segment II dark brown or fuscous 2
– Pronotum pale; antennal segment II pale, sometimes with apex or base fuscous 3
2. Antennal segment II distinctly longer than basal width of the pronotum; male genital capsule without a tubercle above left paramere . . . . . *D. gracilentus* Parshley
– Antennal segment II distinctly shorter than basal width of the pronotum; male genital capsule with a distinct tubercle above left paramere . . . . . *D. vestitus* Uhler
3. Length of antennal segment I nearly equal to width of head across eyes; antennal segment II reddish brown to fuscous at base and apical ¼; hemelytra always macropterous . . . . . *D. famelicus* (Uhler)
– Length of antennal segment I shorter, subequal to width of vertex, plus diameter of one eye; antennal segment II pale basally, narrowly reddish brown or fuscous only on apical ⅕ or less; hemelytra brachypterous or macropterous . . . 4
4. Antennal segment I fuscous to black; antennal segment II subequal to basal width of pronotum . . . . . *D. hesperus* Knight
– Antennal segment I mostly pale; antennal segment II distinctly longer than basal width of pronotum . . . . . *D. discrepans* Knight

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DESCRIPTIONS OF IMMATURE STAGES OF SIX *CULICOIDES* LATREILLE SPP. (DIPTERA: CERATOPOGONIDAE) FROM DESERT MOUNTAIN RANGES IN SOUTHERN CALIFORNIA, WITH NOTES ON LIFE HISTORIES AND REARING TECHNIQUE

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Abstract.—Immature stages of six species of biting midges (*Culicoides* spp.) are described from desert mountains in southern California. The eggs, larvae, and pupae of *C. freeborni, C. lahontan, C. boydi,* and *C. cacticola*; the egg and larva of *C. brookmani*; and the egg of *C. utahensis* are described and illustrated. Immature stages described were from primarily laboratory-reared material obtained from gravid, field-collected females to assure a correct association with the adult. Observations on life history and behavior are included.

Key Words: Culicoides, Ceratopogonidae, immatures, morphology

Scientific knowledge concerning adults of biting midges (*Culicoides* spp. Latrielle) is advanced in comparison with what is known of the immature stages. While often collected by aquatic biologists, immature biting midges may not be identified because of their small size, lack of readily distinguishing characteristics, and limited keys. This situation was recently improved through the efforts of Murphree and Mullen (1991) who worked with mostly eastern species of *Culicoides* and compared larval morphology, made descriptions, and developed a key to species. However, the immature stages of western North American *Culicoides* species are poorly known (Blanton and Wirth 1979, Mullen and Hribar 1988, Murphree and Mullen 1991). For example, in the desert mountains of southern California, at least 19 species of *Culicoides* are known to occur (Mullens and Dada 1992a), but the larvae and pupae of only two species had been described. Similarly, the larval habitats for most of these species remained unknown or were presumed.

Knowledge of the larval habitats conveys basic information on where adults originate and whether there are options for controlling pestiferous species at these sites. The ability to recognize the immature forms either in the field or from slide-mounted material eliminates the need for rearing adults solely for diagnostic purposes. Immatures may possess characteristics that allow specific identifications to be made when the adults of certain species are difficult to distinguish. Furthermore, features of the immatures help support some subgeneric concepts previously based solely on adult character states. Thus, the use of immature stages as a taxonomic resource is a useful tool in stabilizing the sytematics of this large genus.

Finally, vector competency is often tested

on laboratory-reared individuals. Understanding the biological processes of these species' immature stages, such as nutritional needs and development time, is crucial to the establishment of laboratory colonies. Some species from this region are suspected vectors of the ruminant pathogen, bluetongue virus (Mullens and Dada 1992a, Wirth and Mullens 1992), thus, detailed information on all life-stages would benefit future vector competency studies.

The objectives of this study were to locate and describe the immature stages of the *Culicoides* species found in the mountain ranges of the Colorado Desert in southern California.

Materials and Methods

Study sites.—Specimens were gathered from the Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, Riverside Co., California (Ting and Jennings 1976) and near the town of Morongo Valley, San Bernardino, Co., California.

Deep Creek is a seasonal stream which contains the drainage from a major area of the north and east slopes of the Santa Rosa Mountains. Apart from those species that use necrotic cacti as a developmental site, the creek margin was assumed to be a primary larval habitat in this desert environment. Soil emergence traps (n = 6) (Paine and Mullens 1994) were placed in several locations along the margins of Deep Creek, in Deep Canyon, in the spring of 1996. Emerging midges accumulated in 10% NaCl and were later transferred to 70% EtOH.

Several microhabitats were represented along a trapping transect ranging from 300–350 m in elevation, including varying degrees of silt accumulation, mud, and emergent vegetation. After removing insects from the trap head on each sample date, the trap was moved one trap-diameter along the transect so that a new section of undisturbed creek margin was sampled. Samples were processed using a stereomicroscope, and midges in the genus *Culicoides* were identified to species using Wirth et al. (1985) and reference material from the UC Riverside Entomology Collection.

Extraction of larvae from substrate.—Biting midge larvae were field-collected, returned to the laboratory and held for emergence. Small samples of larval habitat were taken and larvae extracted using agar (Kline et al. 1981) or by direct salt-flotation in saturated magnesium sulfate solution (Kettle and Lawson 1952).

Extracted larvae were reared on nutrient-enriched 1.5% noble agar plates (addition of nutrient broth) at laboratory temperatures ranging from 21–25°C. Larvae were offered several food sources, including a nutrient rich liquid diet consisting of bacteria, algae, and yeast used for rearing colonized *Culicoides variipennis sonorensis* Wirth and Jones (Jones et al. 1969). In addition, the bacterial feeding nematodes, *Pelodera* sp. and *Panagrellus redivivus* (L), were supplied as potential prey on a biweekly basis (Mullens and Velten 1994). Larvae were not reared in the collected substrate because it was impossible to observe larval behavior or recover exuviae. In contrast, the agar was essentially transparent and allowed for direct observation of behavior, number, and stage of the developing larvae. Also, potential predators could be excluded. Disadvantages of using an artificial rearing medium include the possible loss of beneficial elements found in the natural substrate (i.e., important nutrients, physical characteristics)

Kettle and Lawson (1952) described two methods for associating the larva and adult of a species. In the first procedure, eggs from an identified female are collected and reared in monoxenic culture. In the second method, field-collected larvae are grouped together by shared characters and held until the adults emerge and are identified. The second method has commonly been used but is completely trustworthy only when homogeneous collections are made or when individual exuviae are associated with an adult; otherwise misidentifications are pos-

sible. To minimize this possibility, laboratory-reared larvae from identified isofemale lines were used whenever possible. This was carried out by collecting host-seeking females in CDC-type battery powered suction traps (Sudia and Chamberlain 1962) baited with ~1 kg of dry ice (CO_2). Traps were set ~1 hour before dusk and retrieved ~1 h after dawn.

Material used in the descriptions of immature stages was mostly reared in the laboratory from field-trapped females as described by Breidenbaugh and Mullens (1999). Collected females were given the opportunity to feed on blood through an artificial membrane. A Parafilm or chick-skin membrane and defibrinated sheep blood were used with a temperature-controlled, water-jacketed feeder (Hunt 1994). Engorged females were separated from other midges in the collections while immobilized on a chill table. Female midges were then held at 21°C for 7 days. Some females would oviposit on their own, onto damp filter paper, when held overnight in a Petri dish. However, decapitation of females to induce oviposition was generally required. The filter paper with eggs from an individual female was placed on a 1.5% agar plate and held in a humid chamber. Eggs were checked daily for hatch. First-instar larvae were offered the same food types as described for field-collected larvae. A sample of eggs was placed into 70% EtOH for later examination by scanning electron microscopy (SEM). The parental adult female was preserved in 70% EtOH and later slide-mounted in balsam after Wirth and Marston (1968), and determined to species.

Preparation of eggs.—Eggs were fixed in alcoholic Bouin's fixative (Day et al. 1997) [80% ethanol (150 ml), concentrated formalin (60 ml), glacial acetic acid (15 ml), picric acid crystals (1 gm)], for 30 minutes, washed in 20% EtOH and then dehydrated through an EtOH series. Specimens were critical-point dried, transferred onto stubs backed with sticky tape, sputter coated with gold-palladium, and viewed on either a JOEL JSM-35C or a Phillips XL30 scanning electron microscope.

Preparation of larvae.—Developing larvae were observed daily for feeding behavior and growth. Fourth-instar larvae were killed in 70% EtOH. A few cultures were allowed to mature so that developmental data could be obtained. Larvae were mounted on microscope slides in either Hoyer's medium, Canada balsam, or Euparal. Most larvae were placed ventral side up to facilitate examination of the epipharyngeal combs. Other larvae were mounted dorsally and laterally; head capsules of some larvae were dissected. Slide-mounted specimens were examined at 125×, 312×, 500×, and 1,000× (oil immersion) using bright-field and/or phase-contrast microscopy as needed.

Larvae were measured using a reticle placed in the eyepiece of a Zeiss compound microscope, and were illustrated with the aid of a *camera lucida*. The following measurements were made from fourth-instar larvae of 5 species, after Murphree and Mullen (1991): total length (TL), head length (HL), head width (HW), subgenal width (SGW), mandible length (ML), width across the lateral arms of the epipharynx (LAW), total width across the paired dorsal comb sclerites of the epipharynx (DCW), caudal-segment length (CSL), caudal-segment width (CSW), length of setae 'o' (OL), and the distance between their bases (OD). Total length was not measured by Murphree and Mullen (1991).

From values listed above, the following ratios were calculated: head ratio (HR = HL/HW), subgenal ratio (SGR = HW/SGW), and caudal-segment ratio (CSR = CSL/CSW). Illustrations were made of the structures and chaetotaxy of the head capsule and caudal segment when possible. The hypostoma, epipharynx, hypopharynx, and mandible were illustrated where visible in the head capsule. Thoracic pigmentation and anal papillae were drawn when appropriate.

Preparation of pupae.—Pupae were col-

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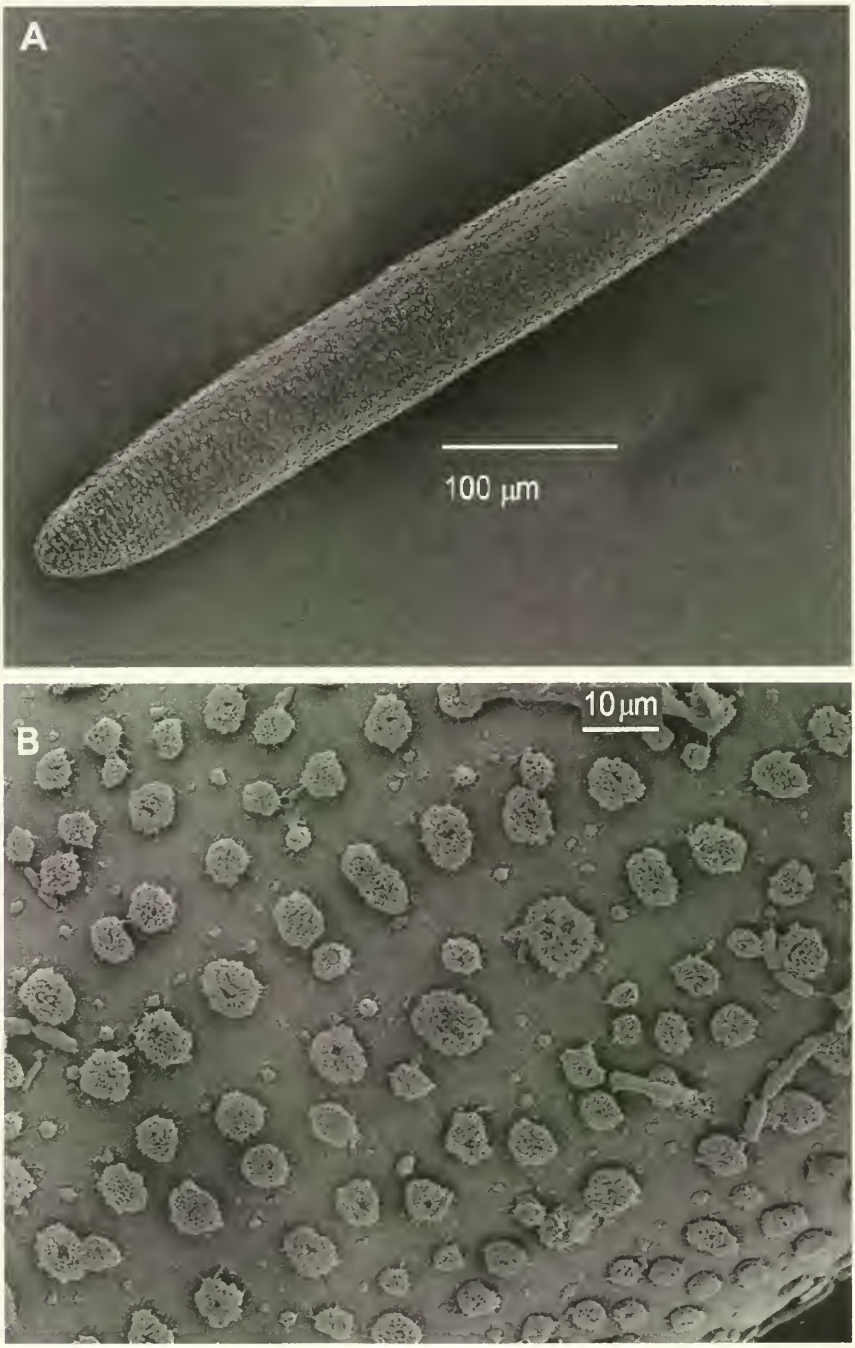

Fig. 1. *Culicoides freeborni*, egg. A) Lateral view of entire egg. B) Detail of egg surface.

lected from laboratory cultures. Pupae were placed individually into 1.5 dram vials on filter-paper over saturated cotton. Organdy mesh lids allowed air-exchange but prevented escape of emerging adults. After adult emergence, the pupal exuviae were placed in 75% EtOH and slide-mounted in Hoyer's or Canada balsam. Whole pupae were placed in EtOH followed by 10% KOH for 24–48 hours prior to mounting.

Pupae were dissected and mounted so that the respiratory horns were seen in lateral view, the operculum in dorsal view, cephalothorax and abdomen in lateral or dorsal view, and the caudal segment in dorsal or ventral view. Pupae were viewed under the same conditions listed above for larvae and the following structures were described and illustrated: respiratory horn, operculum, caudal segment, and the *ad, dl, dasm, dpm, lasm, lpm,* and *vpm* tubercles. Chaetotaxy is reported from the fourth abdominal segment.

Morphological terminology follows Becker (1961) and Campbell and Kettle (1975) for eggs, Murphree and Mullen (1991) for larvae, and Lamberson et al. (1992) and Nevill and Dyce (1994) for pupae.

Voucher specimens of all taxa were deposited in the University of California, Riverside Entomology Research Museum. Immature stages associated with an isofemale were coded with the same collection code and with a series number (e.g., the second adult female collected from Morongo Valley on 9 June 1996 is coded M.V. 9-VI-96 A2). The total number of specimens examined is given in parentheses in the material studied sections.

Results

The immatures of a total of eight *Culicoides* species, representing four subgenera and one unplaced species group, were described or reared for one or more life-stages. The taxa are described in systematic order after Wirth et al. (1985). Descriptions for each life stage follow the pattern of egg, larva, and pupa, if available. Information on larval or pupal behavior and rearing is given for five species. A discussion of the morphology and biology of each species is also included.

The eggs of six species are described for the first time using SEM techniques. Descriptions of larvae are those of the fourth-instar. The larvae of five species are described and illustrated, four for the first time. Larvae have been placed into three groups based on head capsule length: small (<185 μ), medium (190–245 μ), and large (>250 μ) (after Glukhova 1979, Murphree and Mullen 1991). Measurements and ratios for larvae are presented in Table 1. Pupae of four species are described and illustrated for the first time.

Subgenus *Culicoides*

Culicoides freeborni Wirth and Blanton (Figs. 1–5)

Egg.—Cigar-shaped. Surface covered by numerous longitudinal rows of ansulae (Fig. 1A). Secondary, smaller, papillate ansulae, apparently randomly dispersed between and around primary rows. Many rows composed of two separate smaller ansulae; others with only a single larger one. Ansulae thickly stalked, short, with meshwork surface (Fig. 1B). Average length = 405 ± 21 μ, width = 63 ± 9 μ (n = 10).

Larva.—Total length = 5.18 (4.23–6.14) mm. *Head capsule* (Figs. 2A–C): Well-sclerotized, light brown; medium-large, HL = 241 (224–262) μ, HW = 148 (131–166) μ, SGW = 97 (83–102) μ; long and narrow, HR = 1.7 (1.3–2.0); oval-shaped, SGR = 1.5 (1.4–1.6). Mandible (Fig. 2D) medium-large, ML = 54 (46–61) μ; with truncate subapical tooth, base wide. Hypostoma (Fig. 2E) rounded apically, medial margin smooth. Labium well-sclerotized, sagittate. *Epipharynx* (Fig. 2F): Dorsal-comb sclerites with 7–9 unequal angular teeth/sclerite; DCW = 18 (13–20) μ. LAW = 63 (48–77) μ; three combs discernible; comb four with ~12 rounded teeth; middle comb ⅓ as wide as dorsal combs with long, lanceolate teeth.

Table 1. Measurements and ratios (mean ± SE) for *Culicoides* larvae, in micrometers. TL = total length (in mm), HL = head length, HW = head width, SGW = subgenal width, SGR = subgenal ratio, LAW = lateral arm width of the epipharynx, DCW = dorsal comb width, ML = mandible length, CSL = caudal segment length, CSW = caudal segment width, CSR = caudal segment ratio, OL = length of seta "o," OD = distance between setae "o."

	TL	HL	HW	HR	SGW	SGR
C. freeborni	5.18 ± 0.7 (8)	241 ± 14 (12)	148 ± 14 (10)	1.7 ± 0.2 (10)	97 ± 8 (12)	1.5 ± 0.1 (10)
C. lahontan	5.65 ± 0.3 (26)	235 ± 12 (32)	146 ± 9 (29)	1.6 ± 0.1 (29)	93 ± 6 (29)	1.6 ± 0.1 (26)
C. boydi	2.11 ± 0.2 (16)	97 ± 4 (20)	76 ± 5 (18)	1.3 ± 0.1 (18)	48 ± 2 (20)	1.6 ± 0.1 (18)
C. cacticola	2.58 ± 0.1 (8)	120 ± 8 (33)	101 ± 7 (31)	1.2 ± 0.1 (31)	62 ± 5 (34)	1.7 ± 0.1 (31)
C. brookmani	2.85 ± 0.3 (20)	145 ± 6 (37)	88 ± 6 (37)	1.7 ± 0.1 (37)	52 ± 4 (37)	1.7 ± 0.1 (37)

Lateral curtains with several hair-like, thin teeth. *Hypopharynx* (Fig. 2G): wide arms with thin, bilobed hypopharyngeal fringe. *Thoracic pigmentation* (Fig. 2H): brown, elongated arching pattern distributed dorsally and laterally, not touching dorsomedially. *Caudal segment* (Figs. 2I–J): medium length CSL = 470 (418–534) μ, moderately narrow CSW = 227 (160–267) μ, CSR = 2.1 (1.9–2.6). Setae "o" short relative to CSL, OL = 64 (51–70) μ; bases widely separated, OD = 61 (48–72) μ. Anal papillae visible inside caudal segment.

Material studied.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, Morongo Valley, CA. M.V. 19-VI-96 A2 (7). Morongo Valley, CA. M.V. 2-VII-96 A1 (4). Morongo Valley, CA. M.V. 2-VII-96 A2 (3).

Pupa.—Yellow brown. *Respiratory horn* (Fig. 3A): medium brown, relatively short and wide. Scales present over most of horn, absent on apical and basal portions. Lateral spiracular protuberances absent; 6–8 spiracles present distally. *Operculum* (Fig. 3B): brown; spines dark brown, small, rounded; smaller spines present anterior to *am* tubercles; *am* tubercles each with round pore and somewhat narrow spine; distinct rounded tubercle present at base of operculum. *Caudal segment* (Fig. 3C): band of spines along anterior margin, "V-shaped" band medially. Posterolateral processes with middle portions covered by spines, smooth apically. *Chaetotaxy*: Dorsal tubercles (Fig. 3D): 1, 2 with medium length setae; 3 a short spine; 4 a long slender bristle; 5 a round pore. *dl* tubercle (Fig. 3E): with three slender, unequal bristles. *Abdomen* (Fig. 3F): *dasm* tubercles: one with short hair, other with medium spine. *dpm* tubercles: 1 with medium length bristle; 2 a slender bristle; 3–5 spinate with relatively thick spines. *lasm* tubercle: spinate; medium length bristle. *lpm* tubercles: spinate; 1, 3 slender bristles nearly equal; bristle 2 longer, more slender than 1, 3. *vpm* tubercles: rounded; 1, 3 slender, nearly equal spines; 2 with long slender bristle.

Material studied.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, Morongo Valley, CA; M.V. 19-VI-96 A2 (3).

Behavior and rearing.—Larvae are predatory on nematodes, and were observed aggressively feeding on *Panagrellus redivivus*. As with *Culicoides lahontan* Wirth and Blanton, *Culicoides freeborni* head capsule size is smaller than other species in the subgenus *Culicoides* as reported in Murphree and Mullen (1991). Although larvae appear to do well in agar cultures (e.g., low mortality) a generally smaller larva may have

TABLE 1. Extended.

LAW	DCW	ML	CSL	CSW	CSR	OL	OD
79 ± 12	18 ± 3	54 ± 5	470 ± 45	227 ± 34	2.1 ± 0.2	64 ± 8	61 ± 10
(6)	(8)	(11)	(11)	(8)	(8)	(9)	(4)
63 ± 8	22 ± 2	44 ± 2	451 ± 14	250 ± 19	1.8 ± 0.1	162 ± 47	—
(23)	(19)	(27)	(29)	(22)	(22)	(6)	—
39 ± 2	6	24 ± 1	181 ± 16	110 ± 14	1.6 ± 1.3	21 ± 3	35 ± 2
(18)	(17)	(13)	(18)	(18)	(18)	(14)	(11)
49 ± 6	9 ± 1	32 ± 1	251 ± 14	128 ± 13	2.0 ± 0.2	24 ± 8	54 ± 18
(33)	(16)	(19)	(10)	(10)	(10)	(5)	(3)
46 ± 4	9	35 ± 2	234 ± 13	119 ± 14	2.0 ± 0.2	55 ± 6	33 ± 4
(25)	(22)	(22)	(27)	(26)	(26)	(17)	(8)

been produced than is typical in feral populations. In the laboratory, females laid an average of 67 ±15 eggs (n = 3 gravid females) with a fertility of 35 ± 21% (n = 3). Eggs hatch in 4 ± 1 days.

Discussion.—The egg, larva and pupa were not previously described. Larvae are difficult to distinguish from *C. lahontan* if measurements are used as the only means of differentiation. Morphologically, the hypopharynx is the most disparate structure between the larvae of the two species. *Culicoides freeborni* lacks two additional sclerotizations found directly anterior to the hypopharyngeal fringe in *C. lahontan*. The anterior margin of the hypostoma of *C. freeborni* is smooth, in contrast to the subapical short teeth found on *C. lahontan*; these appear as short serrations when light microscopy is used. Murphree and Mullen (1991) indicate that the anterior margin is smooth on the hypostomas of two other species (*Culicoides neofagineus* Wirth & Blanton, *Culicoides tristriatulus* Hoffman) in the subgenus *Culicoides*. The pupa of *C. freeborni* is readily separated from pupae in other subgenera in this study by the absence of lateral spiracular protuberances on the respiratory horn. The pupa of this species can be distinguished specifically from the pupa of *C. lahontan* by the thick spines on *dasm* tubercles.

Subgenus *Culicoides*

Culicoides lahontan Wirth and Blanton
(Figs. 4–6)

Egg.—Cigar-shaped. Surface with several longitudinal rows of ansulae (Fig. 4A), but lacking secondary surface features. Ansulae thinly stalked expanding apically into wide meshwork surface, several with central pore (Fig. 4B). Average length = 515 ± 41 μ, width = 68 ± 6 μ (n = 10).

Larva.—Total length = 5.65 (4.99–6.80) mm. *Head capsule* (Figs. 5A–C): Well-sclerotized, light brown; medium-large, HL = 235 (214–276) μ, HW = 146 (125–160) μ, SGW = 93 (80–102) μ; long and narrow, HR = 1.6 (1.4–1.8); somewhat oval-shaped, SGR = 1.6 (1.3–1.8). Mandible (Fig. 5D) medium length, ML = 44 (38–48) μ; prominent subapical, slightly curved tooth; somewhat broad apically. Hypostoma (Fig. 5E) rounded apically with medial margin finely dentate. Labium well-sclerotized, sagittate. Epipharynx (Fig. 5F) with dorsal-comb sclerites moderately wide, DCW = 22 (19–29) μ relative to LAW, outer margin of sclerites slightly longer than inner margins; 7–9 teeth/sclerite; teeth wide, pointed, and subequal. LAW = 63 (48–77) μ; comb 4 discernible; lateral curtains, reduced; teeth thin, hair-like. Hypopharynx relatively sclerotized with distinct hypopharyngeal

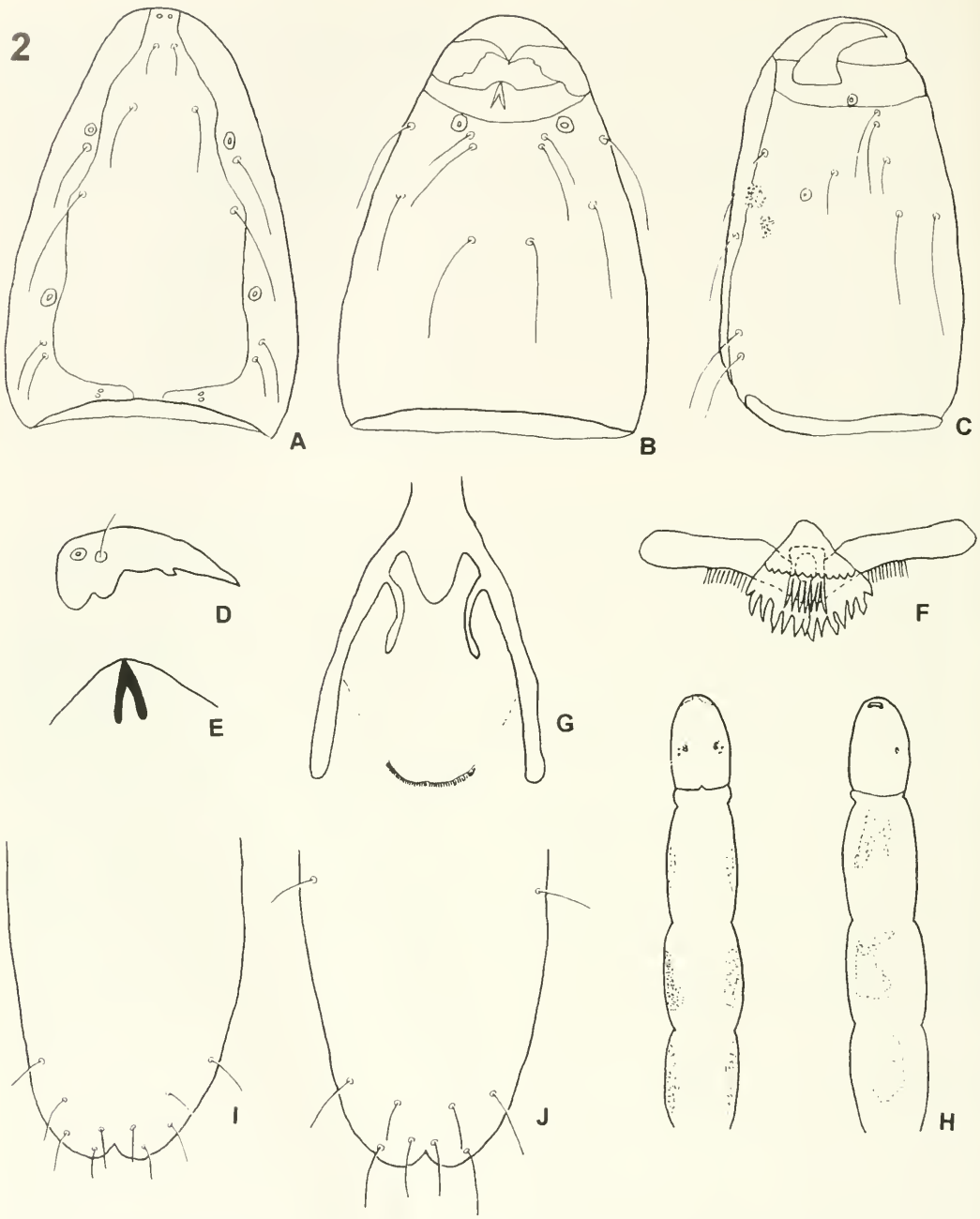

Fig. 2. *Culicoides freeborni*, larva. A) Head capsule, dorsal view. B) Head capsule, ventral view. C) Head capsule, lateral view. D) Mandible. E) Hypostoma. F) Epipharynx. G) Hypopharynx. H) Thoracic pigmentation, dorsal (left) and lateral (right) views. I) Caudal segment, dorsal view. J) Caudal segment, ventral view.

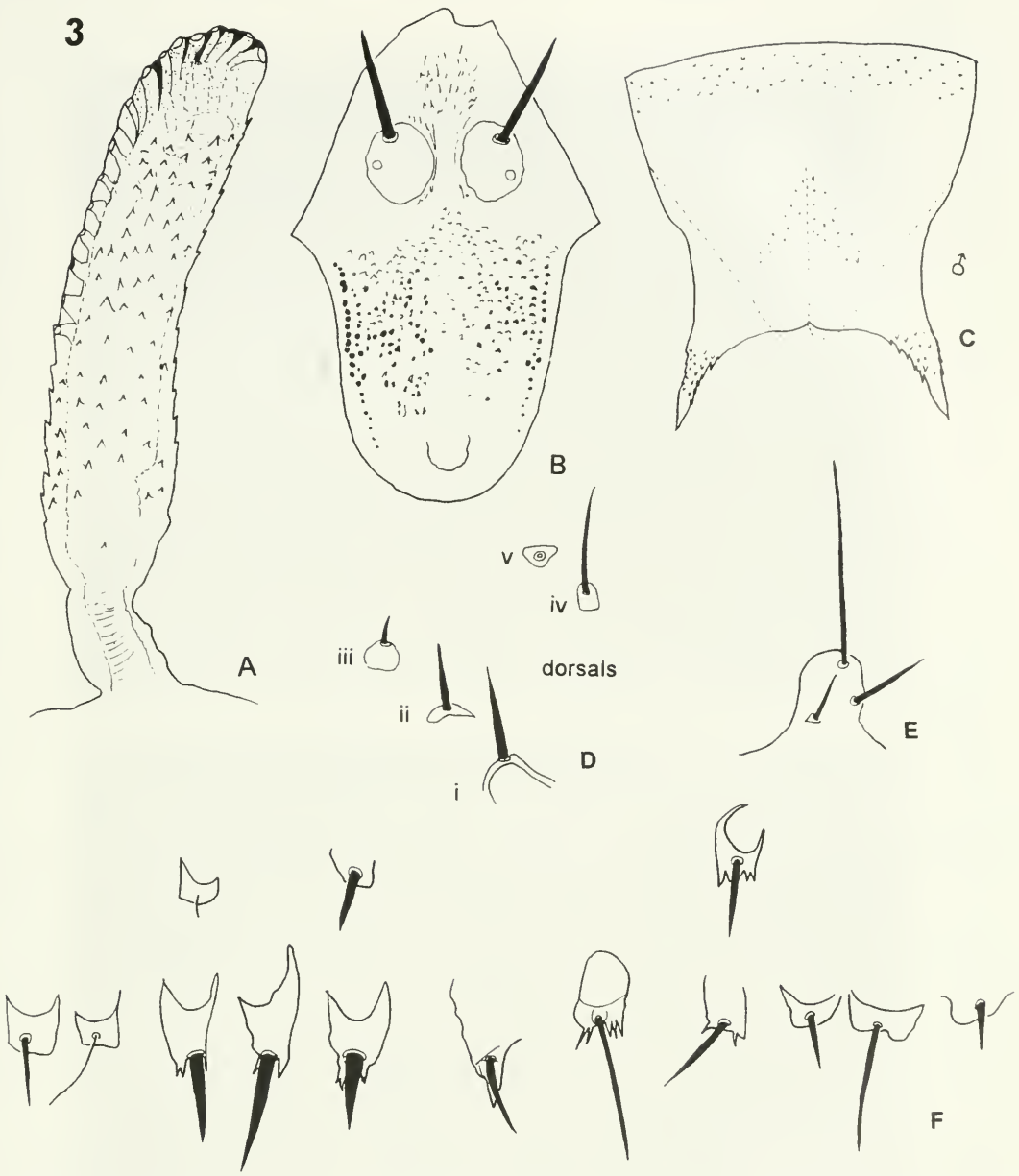

Fig. 3. *Culicoides freeborni,* pupa. A) Respiratory horn. B) Operculum. C) Caudal segment of male. D) Dorsal tubercles. E) *dl* tubercle. F) Abdominal chaetotaxy.

fringe (Fig. 5G). *Thoracic pigmentation* (Fig. 5H): brown pigmentation distributed dorsally and laterally, not touching dorsomedially. *Caudal segment:* medium length, CL = 451 (427–481) μ, moderately wide CW = 250 (223–280) μ, CSR = 1.8 (1.6–2.1). Anal papillae not observed.

Material studied.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, Morongo Valley, CA. M.V. 7-VI-95 A2 (8). Morongo Valley, CA. M.V. 7-VI-95 A6 (11). Morongo Valley, CA. M.V. 7-VI-95 A8 (13). Morongo Valley, CA. M.V. 7-VI-95 A5 (4).

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Fig. 4. *Culicoides lahontan*, egg. A) Lateral view of entire egg. B) Detail of egg surface.

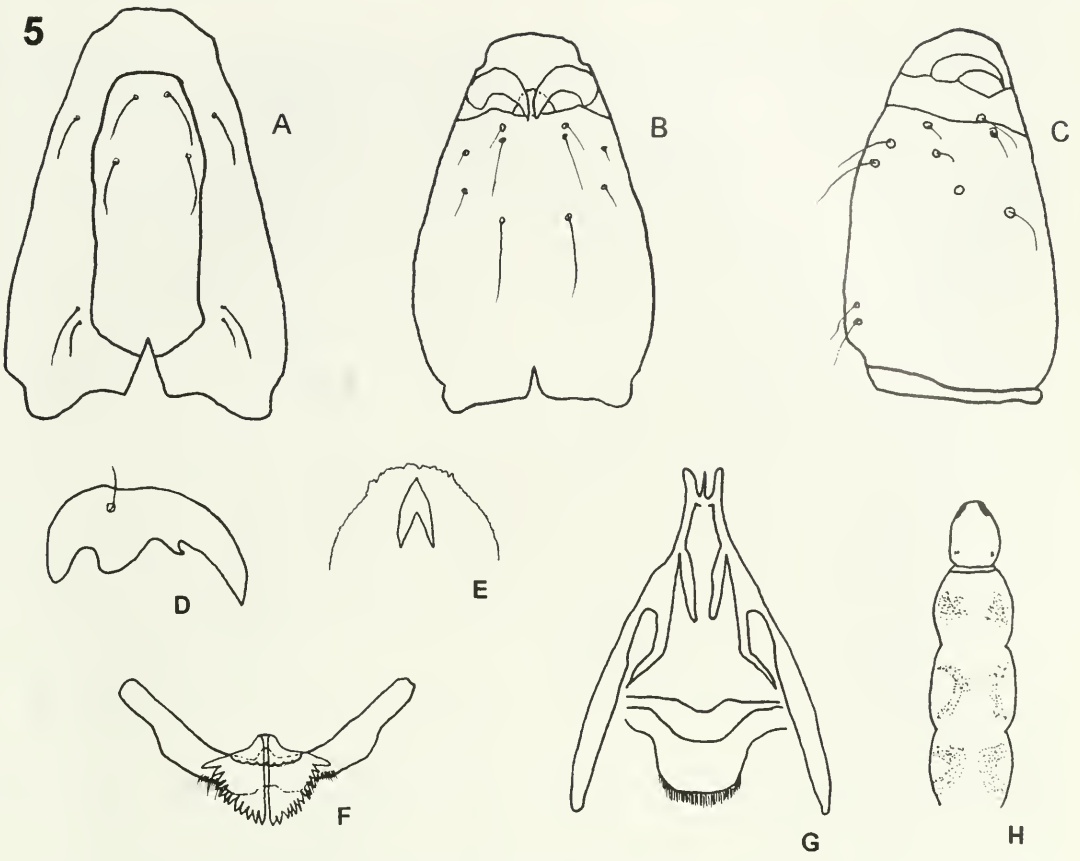

Fig. 5. *Culicoides lahontan,* larva. A) Head capsule, dorsal view. B) Head capsule, ventral view. C) Head capsule, lateral view. D) Mandible. E) Hypostoma. F) Epipharynx. G) Hypopharynx. H) Thoracic pigmentation.

Pupa.—Yellow brown. *Respiratory horn* (Fig. 6A): medium brown; scales present on distal ⅔; lateral spiracular protuberances absent; distal spiracular openings (12–13) present over distal ⅓ of horn. *Operculum* (Fig. 6B): brown; spines dark brown, small, rounded. Spines interspersed with smooth areas; smaller spines occur medially anterior to *am* tubercles; base with dark brown flattened "W." *Caudal segment* (Fig. 6C): with band of spines along anterior margin and "U-shaped" band medially; spines consisting of a rounded tooth with a narrow bristle apically; posterolateral processes covered by sagittate spines, except distal ¼, bare; male and female similar. *Chaetotaxy:* Dorsal tubercles (Fig. 6D): 1–3 spinate; setae 2 longer, more slender than 1; 3 short stout; 4 flattened with long bristle; 5 a round pore. *ad* tubercle (Fig. 6E) with two long slender subequal bristles. *dl* tubercle two slender subequal bristles shorter than *ad* tubercle. *Abdomen* (Fig. 6F): *dasm* tubercles: 1 with slender bristle; 2 longer, more slender. *dpm* tubercles: 1 a short hair; 2, 3 lack protuberances; 4, 5 short slender spines. *lasm* tubercle: spinate; medium length bristle. *lpm* tubercles: spinate; 1, 2 slender bristles nearly equal; 3 bristle longer, more slender than 1, 2. *vpm* tubercles: 1–3 slender, nearly equal bristles.

Material studied.—Laboratory-reared from eggs deposited by individual females collected in San Bernardino County, Morongo Valley, CA. M.V. 7-VI-95 A2 (2). Morongo Valley, CA. M.V. 7-VI-95 A6 (3). Morongo Valley, CA. M.V. 7-VI-95 A8 (4). Morongo Valley, CA. M.V. 7-VI-95 A5 (2).

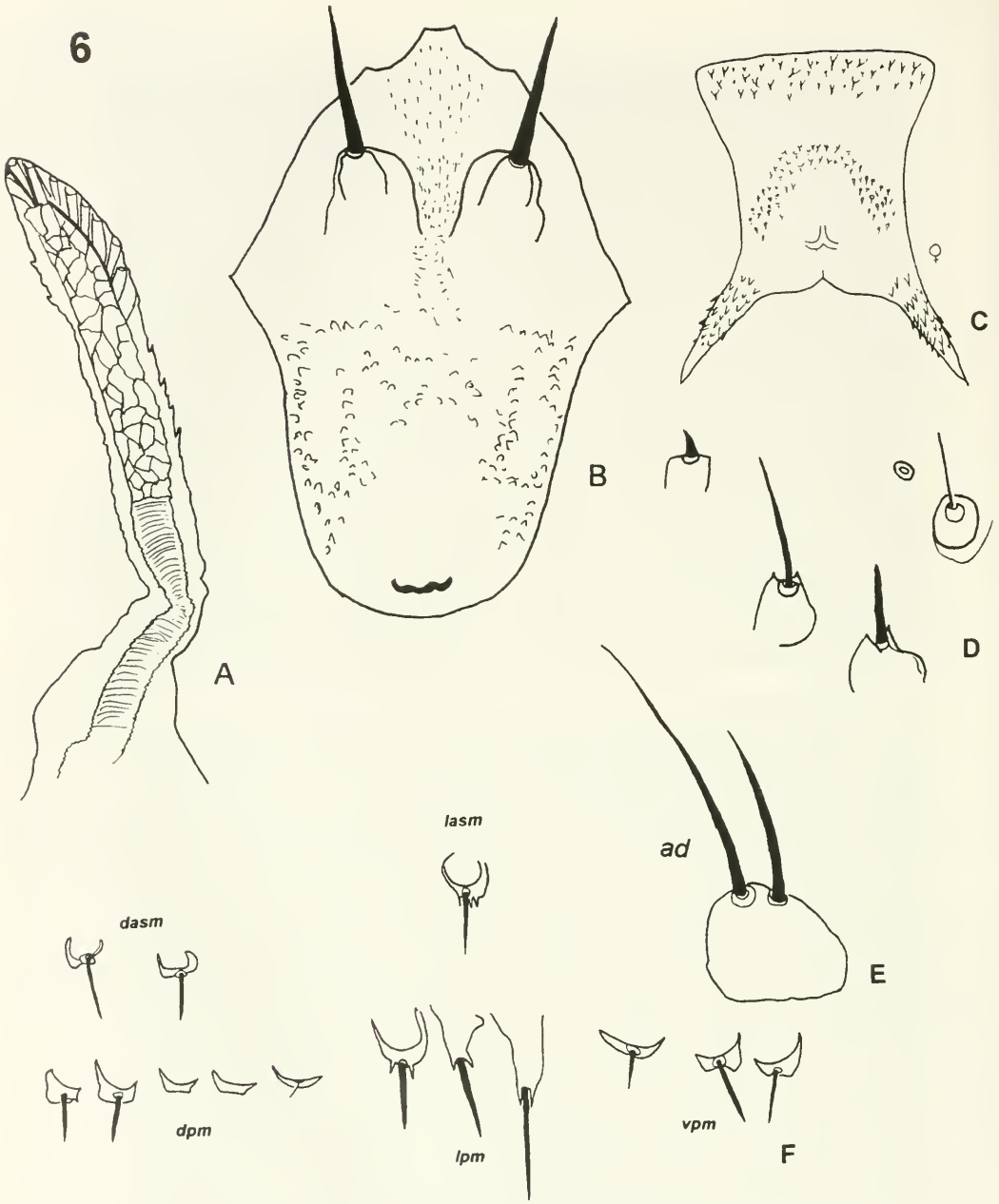

Fig. 6. *Culicoides lahontan*, pupa. A) Respiratory horn. B) Operculum. C) Caudal segment of female. D) Dorsal tubercles. E) *ad* tubercle. F) Abdominal chaetotaxy.

Morongo Valley, CA. M.V. 2-VII-96 A3 (3).

Behavior and rearing.—Adult females were trapped regularly during this study. Mullens and Dada (1992a) encountered large numbers (140/trap/night) of *C. lahontan* in late spring of 1988 at Deep Canyon (a wet year), but relatively few were collected during dry years.

Culicoides lahontan females readily fed

through stretched Parafilm and chick-skin membranes and generally oviposited in the laboratory. In the laboratory, an average of 89 ± 36 eggs were laid (n = 8 gravid females) with a fertility of 55 ± 17% (n = 7). Eggs hatched in 7 ± 1 days. Larvae were observed aggressively feeding on *P. redivivus*. In an individual culture, pupation occurred 60 ± 15 days (n = 14, range 33–68 days) after hatch. The adults emerged 4 ± 1 days (n = 7) later and from this particular culture were all female. A sex bias phenomenon has been observed earlier (see Boorman 1985) with midges reared on agar-based media but the responsible mechanism remains unknown. Pupae are light-tolerant. Adults were recovered from soil emergence traps located along the stream margin of Deep Creek, indicating that stream margins are a developmental site for these midges.

Discussion.—The egg, larva, and pupa were not previously described. Williams (1951) reports short blunt protuberances on the surface of C. *tristriatulus* eggs. This is in contrast to the eggs of *C. lahontan* and *C. freeborni*, which have elongate ansulae. Overall larval head length (HL) of *C. lahontan* and *C. freeborni* is less than that reported by Murphree and Mullen (1991) for the subgenus *Culicoides*, although these species were the largest encountered in the present study. Pupae lack lateral spiracular protuberances as do the pupae of *C. freeborni*. This is apparently a condition of the subgenus as they are also absent in *C. tristriatulus* (Williams 1951) and *Culicoides sommermanae* Wirth and Blanton (Wirth and Blanton 1969). Differential diagnosis of larvae and pupae of this species is treated under the section for *C. freeborni*.

Subgenus *Avaritia*
Culicoides boydi Wirth and Mullens
(Figs. 7–9)

Egg.—Cigar-shaped. Surface with thick rows of ansulae (Fig. 7A), lacking secondary surface features. Ansulae stalks wide at base, narrowing medially, expanding apically into meshwork of equal sized pores (Fig. 7B). Length = 350 μ, width = 38 (n = 1).

Larva.—Total length 2.11 (1.62–2.43) mm. *Head capsule* (Figs. 8A–C): yellow-brown; small, lacking eyespots; mandibles prominently darkened proximally (Fig. 8H); HL = 97 (93–102) μ, HW = 76 (76–83) μ, SGW = 48 (45–53) μ; short, wide HR = 1.3 (1.2–1.4), slightly oblong, SGR = 1.6 (1.5–1.7). Mandible (Fig. 8D), small, ML = 24 (22–26) μ, two separate notched subapical teeth present, base broad with a small seta. Hypostoma (Fig. 8E), smooth medially with single tooth bilaterally. Labium, sagittate, large and distinct. *Epipharynx* (Fig. 8F): LAW = 39 (35–43) μ; DCW = 6 (5–8) μ; with 7 angular unequal teeth/sclerite. Combs 2 and 3 not observed. Comb 4, narrow with 6 angular teeth. Lateral curtains narrow, teeth lancelet, relatively thick. Hypopharynx (Fig. 8G), arms thick, posterior comb reduced, not fringed. *Thoracic pigmentation* (Fig. 8H): equally distributed dorsally in oval patches on thoracic segments. *Caudal segment* (Figs. 8I–J): short, CSL = 181 (154–214) μ, and moderately narrow, CSW = 110 (83–138) μ, CSR = 1.6 (1.4–1.9). Setae "o," short, OL = 21 (18–26) μ, noticeably longer than other caudal setae; OD = 35 (32–38) μ. Anal papillae observed inside caudal segment but never extruded.

Material studied.—Laboratory-reared from eggs deposited by an individual female collected in San Bernardino County, Morongo Valley, CA 14-V-96 A36 (19).

Pupa.—Light brown. *Respiratory horn* (Fig. 9A): light brown; relatively smooth, 3–4 lateral, 5–7 apical spiracular openings present; color darkening along extreme apex; reticulation pattern visible above first lateral spiracular opening. *Operculum* (Fig. 9B): spines extremely elongated into hair-like processes that extend beyond opercular margins; spines not present beyond narrow *am* tubercles; prominent tubercle present at base of operculum. *Caudal segment* (Fig. 9C): Spines, relatively large, tapering into

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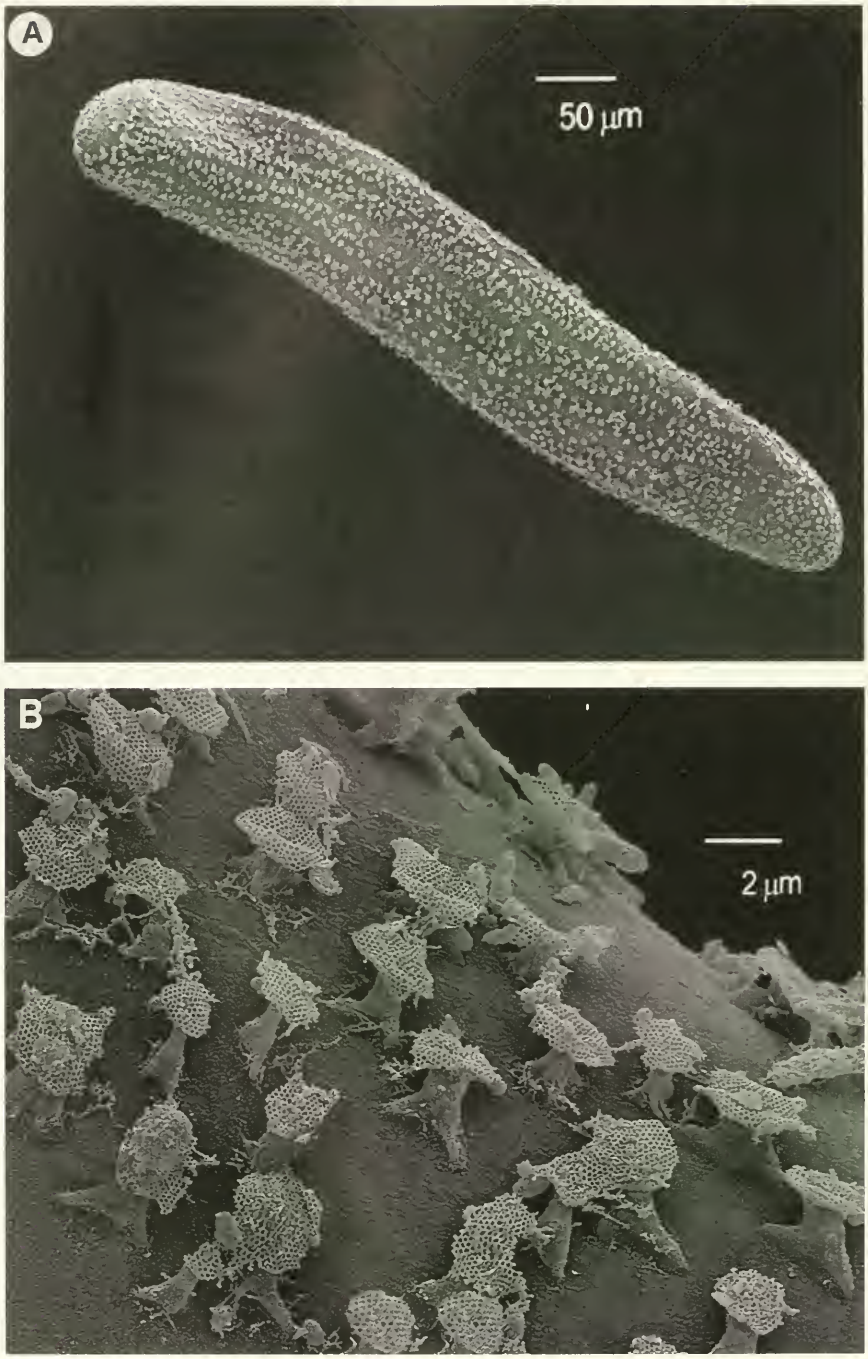

Fig. 7. *Culicoides boydi*, egg. A) Lateral view of entire egg. B) Detail of egg surface.

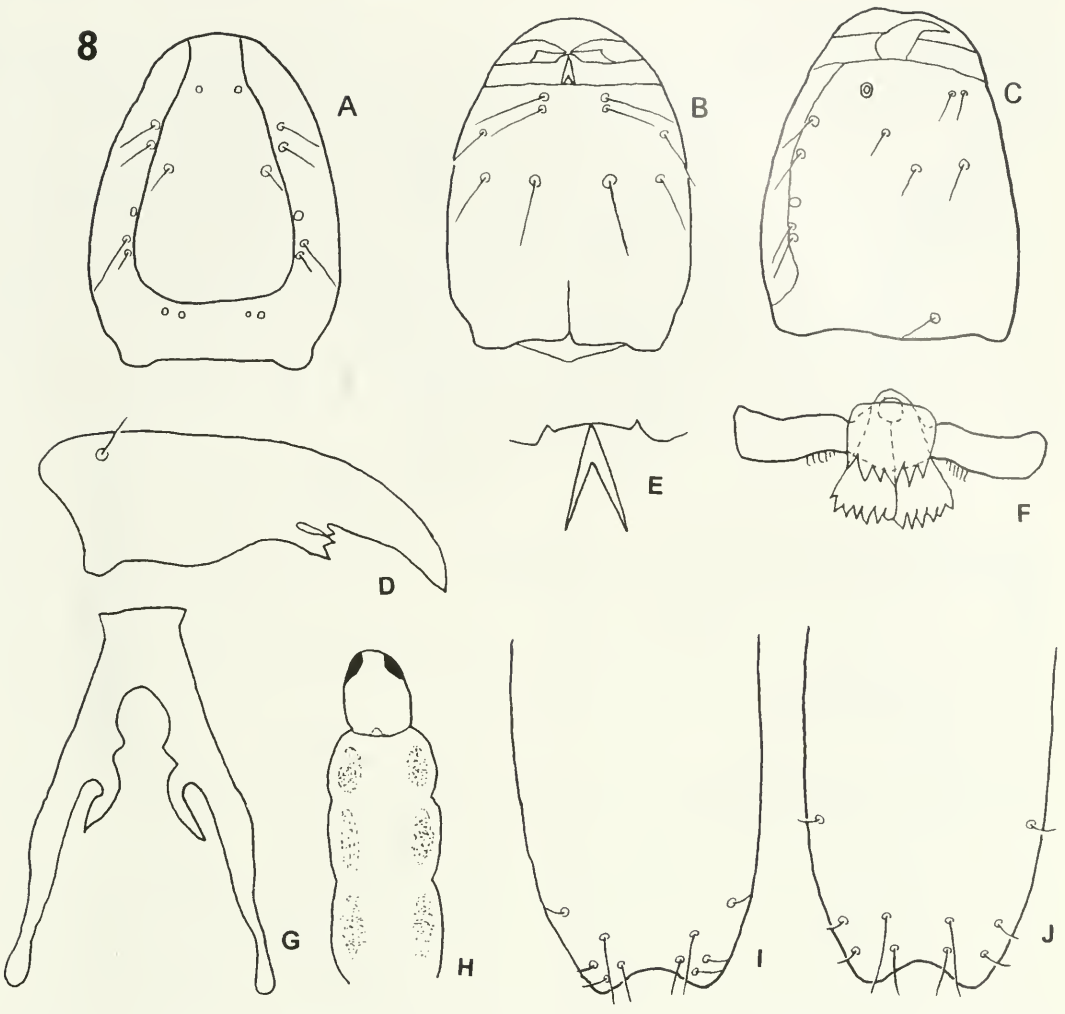

Fig. 8. *Culicoides boydi,* larva. A) Head capsule, dorsal view. B) Head capsule, ventral view. C) Head capsule, lateral view. D) Mandible. E) Hypostoma. F) Epipharynx. G) Hypopharynx. H) Thoracic pigmentation, dorsal view. I) Caudal segment, dorsal view. J) Caudal segment, ventral view.

short hair-like processes; wide band of spines present anteriorly, "U-shaped" band dorsomedially, and along the posterior margin of the posterolateral processes; genital sheaths extending beyond segment margin. *Chaetotaxy:* Dorsal tubercles (Fig. 9D): 1–4 with spines; 1, 3 short, stout; 2 longer; 4 spinate with long, thinner spine; 5 a round pore. *ad* tubercle (Fig. 9E) two long hair-like setae, one short thicker spine. *dl* tubercle with two slender subequal spines (Fig. 9F). *Abdomen* (Fig. 9G): *dasm* tubercles: 1 a short slender spine, 2 a long bristle. *dpm* tubercles: 1, 2, and 4 tubercles absent; 3 with short hair; 5 a short bristle. *lpm* tubercles: 1, 3 spinate with short spine; 2 spinate with long bristle. *lasm* tubercle: spinate with long bristle. *vpm* tubercles: 1, 3 with short spine; 2 a long slender spine.

Material studied.—Laboratory-reared from eggs deposited by individual female collected in San Bernardino County, Morongo Valley, CA 14-V-96 A36 (10).

Behavior and rearing.—A single *C. boydi* female provided the offspring for the morphological measurements reported here.

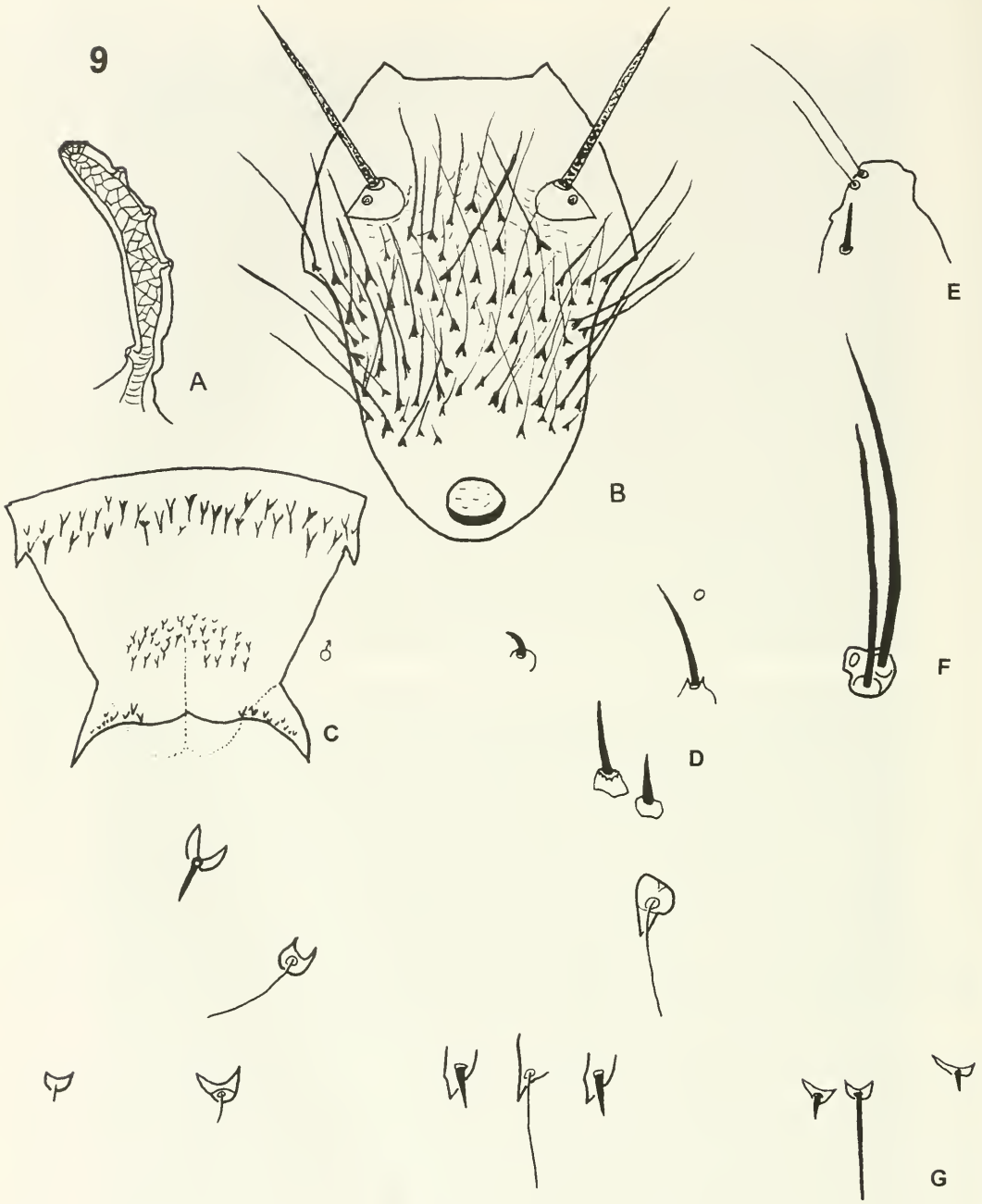

Fig. 9. *Culicoides boydi*, pupa. A) Respiratory horn. B) Operculum. C) Caudal segment of male. D) Dorsal tubercles. E) *ad* tubercle. F) *dl* tubercle. G) Abdominal chaetotaxy.

There were 95 eggs laid which hatched 5 days later. The first pupa occurred in the culture 24 days after egg hatch. Larvae were observed feeding on *Pelodera* sp. nematodes. *Culicoides boydi* was never collected in soil-emergence traps and the developmental site remains unknown. Other species in the subgenus (*Avaritia*) such as

Culicoides chiopterus (Meigen), *Culicoides sanguisuga* (Coquillett), and a *C.* sp. nr. *obsoletus,* in Wisconsin, were found to develop in damp terrestrial habitats (Jones 1961a); it is possible that a functionally similar habitat is used by *C. boydi* in southern California. Females of *C. boydi* have been collected in large numbers (80–100/night) above 500 meters in the Santa Rosa Mountains, CA (Mullens and Dada 1992a) and up to 280/night have been taken at other higher elevation desert habitats (Wirth and Mullens 1992). *Culicoides boydi* is a suspected vector of BTV to bighorn sheep because of the habitat overlap and seasonal abundance during spring lambing; host affinity is presumed to be mammals. These midges bit the first author on at least two occasions at the Morongo Valley site and other records of biting humans are known (Mullens and Dada 1992b, Wirth and Mullens 1992).

Discussion.—Adults of this species were recently described from western Riverside County, California by Wirth and Mullens (1992), but the egg, larva and pupa were previously unknown. Larvae are characteristic of the subgenus *Avaritia.* A well-sclerotized labium, thoracic pigmentation in lateral oval patches, and the presence of only two sets of combs are typical larval characteristics of this subgenus (Murphree and Mullen 1991). The pupa of *C. boydi* is also characteristic of the subgenus *Avaritia.* The opercula of this subgenus possess spines that are elongated into hair-like processes. The pupa of *C. boydi* is very similar to pupa of a n. sp. of *Culicoides* nr. *obsoletus* (Jones 1961b) from Wisconsin, the latter was never formally described. Jamnback and Wirth (1962) reviewed British, Wisconsin, and New York specimens and indicated that the three collections represent the same species. Kettle and Lawson (1952) specify only 1 *dpm* tubercle for *C. chiopterus* and *C. obsoletus* from Britain, while Jones (1961b) reports 2 *dpm* tubercles on the Wisconsin species. However, Jamnback and Wirth (1962) found that the dorsal posterior marginal tubercles were variable in the groups, with either one or two present on the fourth abdominal segment. *Culicoides boydi* has two *dpm* tubercles on segment four.

Subgenus *Drymodesmyia*

Culicoides cacticola Wirth and Hubert

(Figs. 10–12)

Egg.—Cigar-shaped. Surface with longitudinal rows of ansulae often incomplete (Fig. 10A). Secondary surface features lacking. Ansulae, rounded papillae without meshwork surfaces (Fig. 10B). Average length = 281 ± 24 μ, width = 59 ± 7 μ (n = 11).

Larva.—Total length = 2.58 (2.45–2.84) mm. *Head capsule* (Figs. 11A-C): yellow, small. HL = 120 (99–133) μ, HW = 101 (90–117) μ, SGW = 62 (54–70) m; short, broad, somewhat oval; HR = 1.2 (1.0–1.3), SGR = 1.6 (1.5–1.9). Mandible (Fig. 11D) small, ML = 32 (30–35) μ, curved, pointed apically, with process formed by two parallel bluntly pointed teeth free from inner margin; mandibular seta set in groove. Hypostoma (Fig. 11E) smooth medially, with large tooth and several serrations laterally. *Epipharynx* (Fig. 11F): with LAW = 51 (46–62), dorsal combs narrow relative to LAW. DCW = 9 μ (n = 16), with 8 wide, pointed, subequal teeth; only 2 epipharyngeal combs clearly visible; comb 4 with 10–12 short teeth; lateral curtains narrow with up to nine short teeth. Hypopharynx (Fig. 11G) with posterior comb fringed. *Thoracic pigmentation:* absent. *Caudal segment* (Figs. 11H–I): moderately oblong, CSL = 251 (236–276) μ, CSW = 128 (107–143) μ, CSR = 2.0 (1.7–2.3). Setae thin, short, OL = 24 (13–35) μ; OD = 54 (37–67) μ. Three pairs of bifurcate anal papillae within caudal segment never observed extruded.

Material studied.—Collected from rotting barrel cactus Riverside County, Palm Desert, CA. 10-IV-95 (4); laboratory-reared from eggs deposited by individual females collected in Riverside County, Palm Desert,

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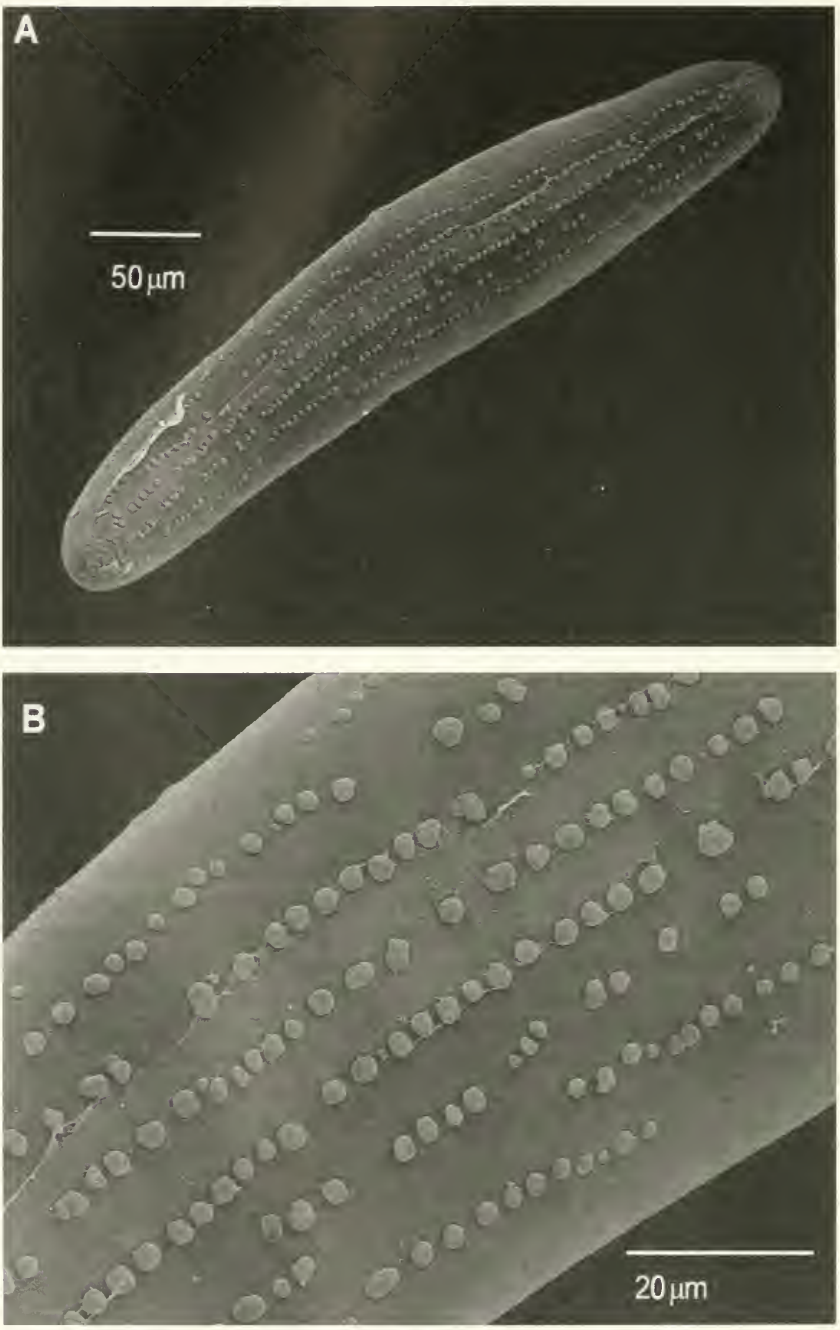

Fig. 10. *Culicoides cacticola*, egg. A) View of concave surface of entire egg. B) Detail of egg surface.

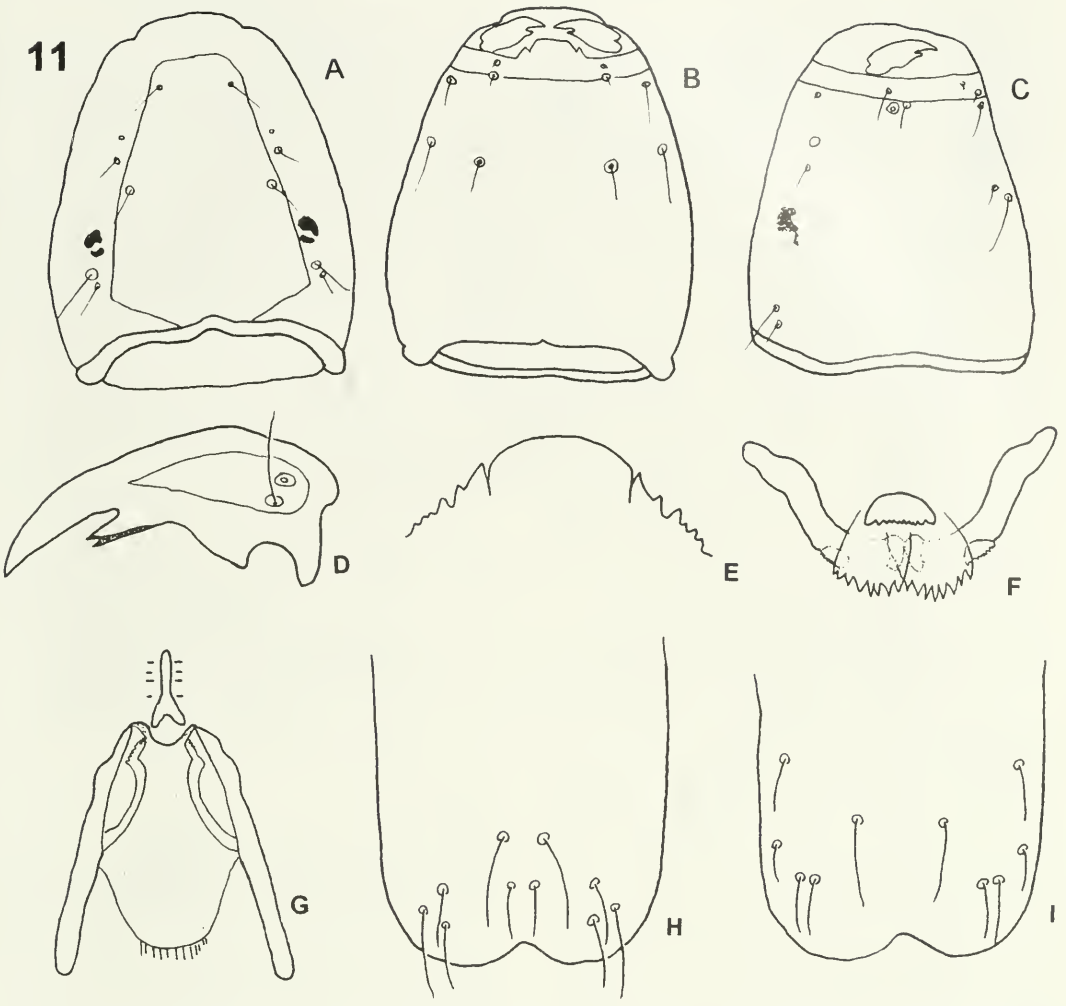

Fig. 11. *Culicoides cacticola*, larva. A) Head capsule, dorsal view. B) Head capsule, ventral view. C) Head capsule, lateral view. D) Mandible. E) Hypostoma. F) Epipharynx. G) Hypopharynx. H) Caudal segment, dorsal view. I) Caudal segment, ventral view.

CA. 9-IV-96 A4 (17); Palm Desert, CA. 17-IV-96 A1 (13); Palm Desert, CA. 17-IV-96 A2 (13).

Pupa.—Yellow. *Respiratory horn* (Fig. 12A): yellow, small; strongly crenulated, with few scales; 3–4 lateral spiracular protuberances present, 6–8 apical spiracles. *Operculum* (Fig. 12B): yellow brown; long, slender, basally stout, spines laterally and medially near *am* tubercles, smaller spines throughout; well-developed *am* tubercles with medium length dark stout spines; large distinct tubercle, lacking setation, located basimedially. *Caudal segment* (Figs. 12C–D): Spines present at base of posterolateral processes, absent apically, both sexes; female with lateral band of spines; male with broad anterior band of spines, genital sheaths not prominent; dorsally, spines found throughout except apical third of posterolateral processes; posterolateral processes moderately separated, both sexes. *Chaetotaxy:* dorsal tubercles (Fig. 12E): 1 rounded, 2 spinate; both with stout spines; 3 with short spine; 4 rounded, with fine bristle; 5 a round pore; *ad* tubercle

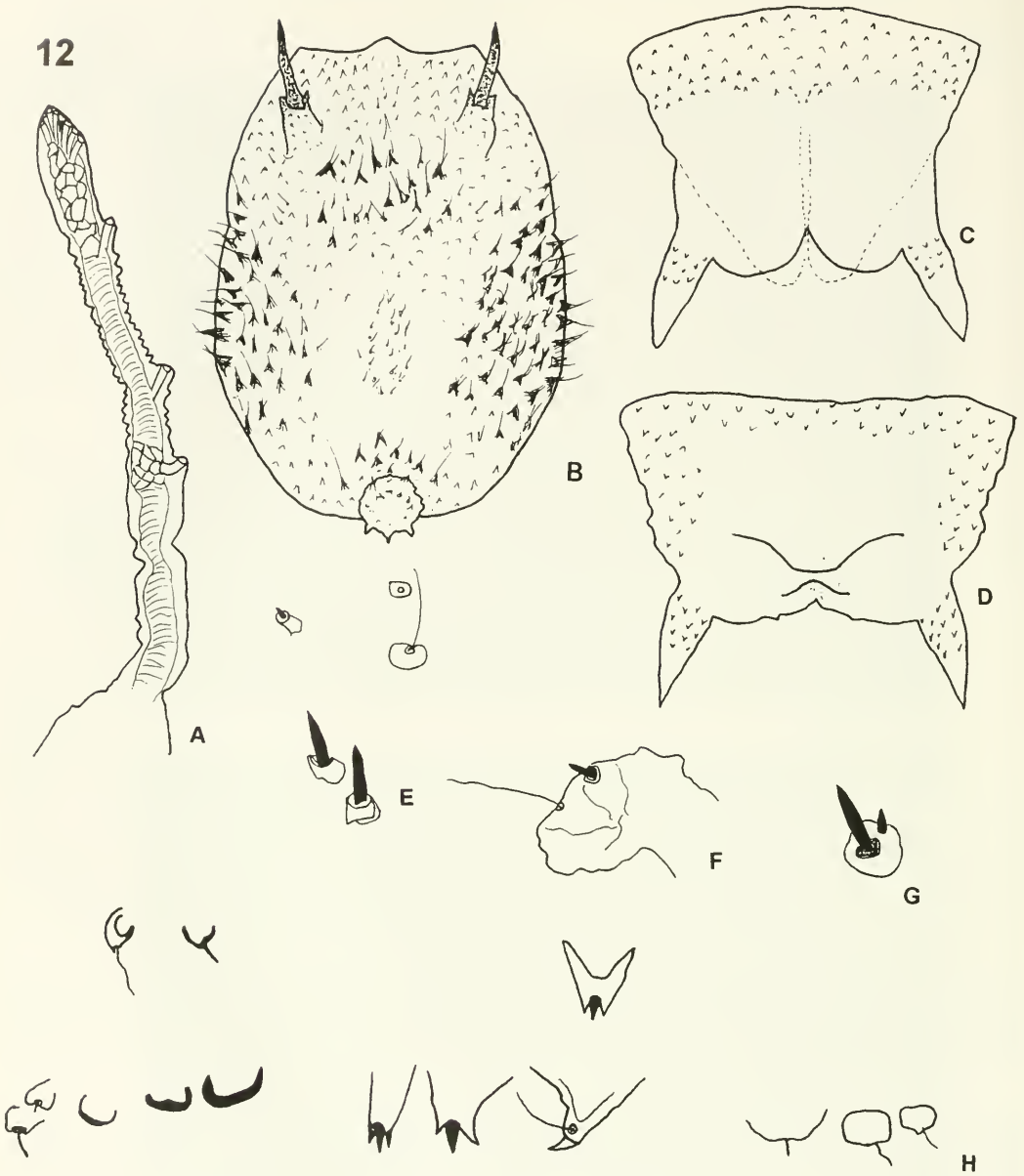

Fig. 12. *Culicoides cacticola*, pupa. A) Respiratory horn. B) Operculum. C) Caudal segment of male. D) Caudal segment of female. E) Dorsal tubercles. F) *ad* tubercle. G) *dl* tubercle. H) Abdominal chaetotaxy.

(Fig. 12F): large, with short stout spine and long slender bristle; *dl* tubercle (Fig. 12G): with two stout spines, one medium length, one short. *Abdomen* (Fig. 12H): *dasm* tubercles rounded; 1 with slender bristle; 2 with thick hair; *dpm* tubercles: 1, 2 with hairs; 2 shorter; 3–5 rounded, lacking setation; *lasm* tubercle: spinate; short stout spine; *lpm* tubercles: spinate; 1 with slender bristle; 2, 3 short stout spines; *vpm* tubercles: 1–3 rounded, with short slender bristles.

Material studied.—Laboratory-reared from eggs deposited by individual females

collected in Riverside County, Palm Desert, CA. D.C. 4-19-96 A2 (3); Palm Desert, CA. D.C. 4-19-96 A4 (2); Palm Desert, CA. D.C. 4-19-96 A5 (3).

Behavior and rearing.—Gravid females were collected with suction traps using rotting cactus as bait and allowed to oviposit in the lab. Another species in this subgenus (*Drymodesmyia*), *C. ryckmani* Wirth and Hubert, also collected at rotting cactus, oviposited in the lab but the eggs failed to hatch. Larvae of *C. cacticola* were predaceous on both species of nematodes offered as food. One culture was reared, from egg to adult, entirely on *P. redivivus* nematodes as the sole food source. Pupae are negatively phototaxic and possess the ability to move down into the agar substrate. In the laboratory, females laid an average of 103 ± 60 eggs with a fertility of 93% ± 13 (n = 8 gravid females). Eggs hatched in 3 ± 1 days. Pupation occurred 19 ± 2 days (n = 42) after hatch. Adults emerged 3 ± 0.6 days (n = 38) later with a sex ratio of 31:7, m:f.

Discussion.—The egg and pupal stages previously unknown. The larva was first described by Murphree and Mullen (1991) from material taken from the Deep Canyon site, but is expanded here with a larger series and added developmental data. These midges use necrotic cacti as a larval development site. The most common cactus utilized by the midges, within the study area, was the barrel cactus (*Ferocactus cylindraceus*).

This species was originally described as *C. cacticolus* by Wirth and Hubert (1960); however, the suffix -cola is a neutral term and did not need to agree with the masculine ending of *Culicoides*. The name was corrected in Wirth et al. (1985) and Borkent and Wirth (1997).

The present study agrees with measurements reported by Murphree and Mullen (1991), in general, although the overall shape of the head capsule is presented as less triangular here. Furthermore, they illustrate dorsal comb 2, whereas it was so indistinct in material from this study that it is not shown. The dorsal comb widths are in perfect agreement. The caudal segment descriptions vary between studies. Here the caudal segment is presented as more oblong (CSR = 2.0) rather than rounded (CSR = 1.3).

Discrepancies between studies are partially a result of the small number of specimens measured (2) in the earlier study, but is better explained by the large number of laboratory reared specimens measured here. A two-sample *t*-test comparing head lengths of field-collected (127 ± 5 μ) versus laboratory-reared larvae (118 ± 8 μ), in this study, found there were significant differences in size (t_{24} = 4.31, P = 0002). This indicates that a strict adherence to morphometrics could be misleading. A combination of qualitative and quantitative data is needed for species identification using laboratory-reared material.

The pupal chaetotaxy reported here is similar to the Lamberson et al. (1992) description of *Culicoides hinmani* Kahalf, a tree-hole breeding species in the subgenus *Drymodesmyia*. *Culicoides hinmani* apparently lacks the distinct basal tubercle on the operculum. Pupae of other cactus breeding *Culicoides* are unknown. It has been suggested that the cactus dwelling *Culicoides* have descended from a tree-hole breeding ancestor (Ryckman 1960, Atchley 1970) which radiated outward from a forest environment to moisture-rich decaying cacti. Future descriptions of immature stages of cactus-dwelling *Culicoides* may help confirm this.

Subgenus *Selfia*
Culicoides brookmani Wirth
(Figs. 13–14)

Egg.—Banana-shaped. Surface smooth, lacking surface structures (Fig. 13). Length = 265 μ, width = 52 μ (n = 1).

Larva.—Total length = 2.85 (2.25–3.20) mm. *Head capsule* (Figs.14A–C): yellow; small, HL = 145 (134–166) μ, HW = 88 (80–106) μ, SGW = 52 (48–61) μ; rela-

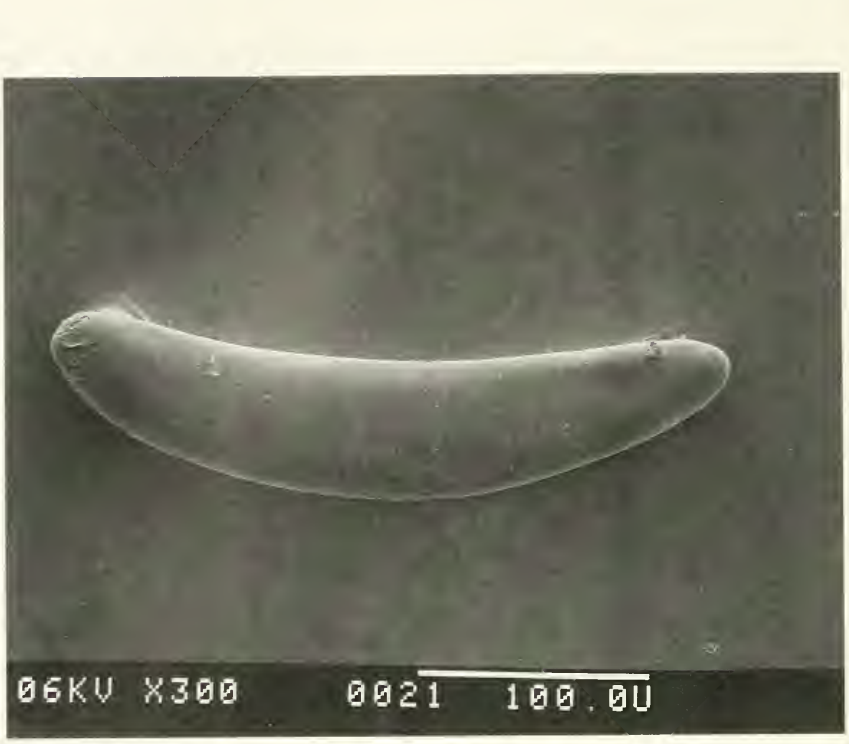

Fig. 13. *Culicoides brookmani*, lateral view of entire egg.

tively long, narrow, HR = 1.7 (1.4–1.9), oblong SGR = 1.7 (1.5–1.9). Mandible (Fig. 14D) small, ML = 35 (28–39) μ, with distinct subapical notch, associated blunt tooth followed by less distinct second tooth. Hypostoma (Fig. 14E) rounded apically, distinct lateral notches and appressed teeth. Labium absent. *Epipharynx* (Fig. 14F): two combs present; DCW = 9 (8–11) μ, each sclerite with 7 moderately equal angular teeth; comb 4, broad, wide equal to DCW, dorsal combs with 8–9 equal angular teeth; lateral curtains reduced. LAW = 46 (37–54) μ. *Hypopharynx* (Fig. 14G): arms narrow, posterior comb distinctly serrated. *Thoracic pigmentation* (Fig. 14H): faint but consistent among individuals; dorsally restricted to collar of prothoracic segment, forms hourglass shape on mesothorax, pigment largely complete dorsally on metathorax, also visible laterally and ventrally. *Caudal segment* (Fig. 14I–K): short; CSL = 234 (194–250) μ, moderately narrow, CSW = 110 (83–144), CSR = 2.0 (1.7–2.8); seta "o" relatively short, OL = 55 (48–66) μ, bases moderately separated, OD = 33 (29–38) μ; four deeply bifurcate anal papillae (Fig. 14K).

Material studied.—Collected from margins of Deep Creek, nr. Palm Desert, CA. D.C. 1-III-96 (7); Laboratory-reared from eggs deposited by individual females collected in Riverside County, Palm Desert, CA. D.C. 19-IV-96 (29); Palm Desert, CA. A.H. 10-V-96 (4).

Pupa.—Previously described by Atchley (1970).

Behavior and rearing.—Adults of *C. brookmani* were often collected in emergence traps placed above sandy and silty soil margins of Deep Creek. Larvae and pupae were recovered in soil samples from the same locality. Atchley (1970) recovered many pupae, but no larvae, from a small, shallow, algae-choked stream with slow moving water and soft, red sandy-mud mar-

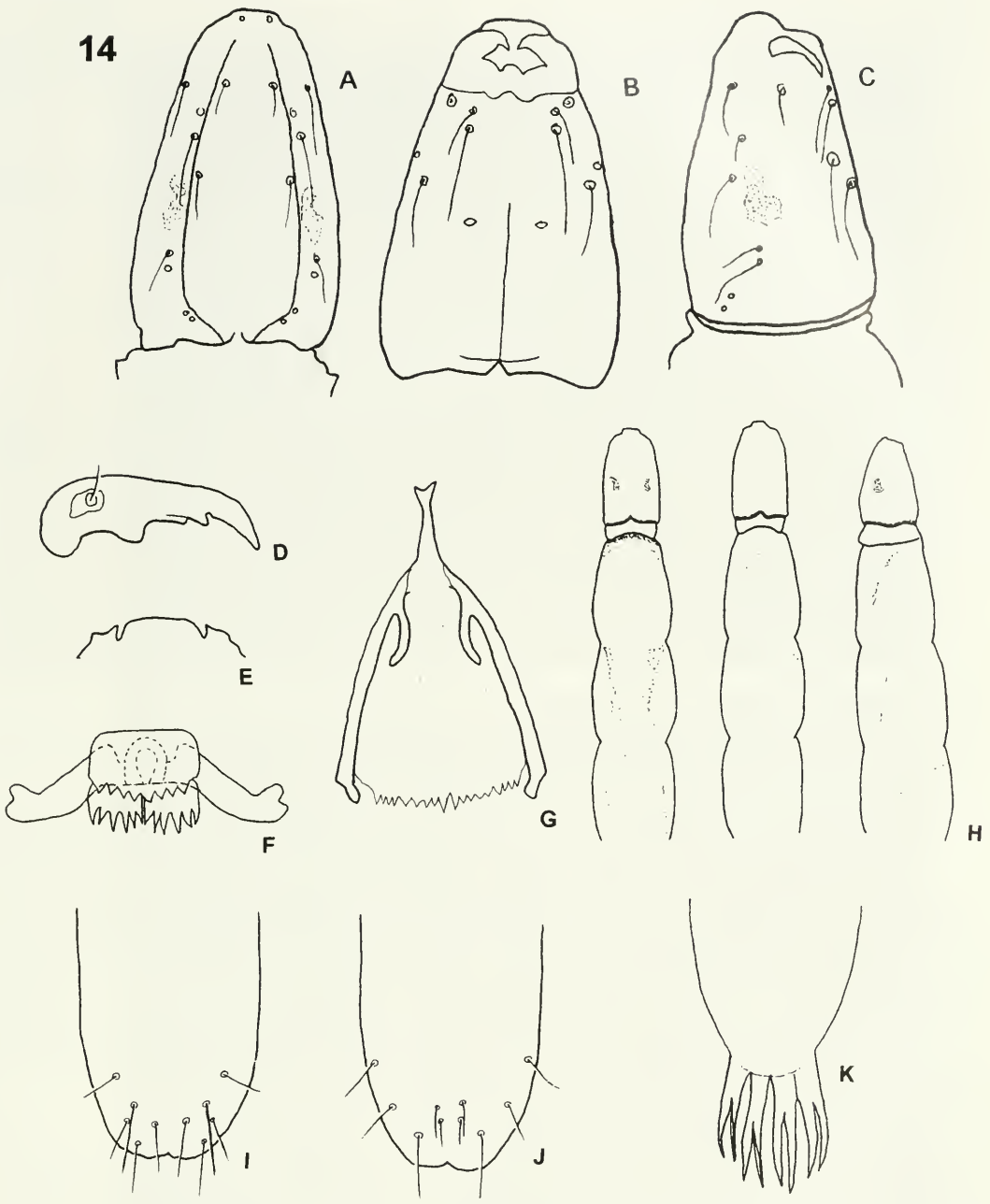

Fig. 14. *Culicoides brookmani,* larva. A) Head capsule, dorsal view. B) Head capsule, ventral view. C) Head capsule, lateral view. D) Mandible. E) Hypostoma. F) Epipharynx. G) Hypopharynx. H) Thoracic pigmentation, dorsal, ventral, lateral views. I) Caudal segment, dorsal view. J) Caudal segment, ventral view. K) Anal papillae, setae not shown.

gins from Arizona. This site description is similar to the Deep Creek site where filamentous algae was present also.

In the laboratory, larvae were observed to feed on *Pelodera* sp. and *P. redivivus* nematodes. A single female laid 94 eggs which hatched 5 days later (27°C); the first pupation event occurred at 13 days.

Discussion.—The larvae were previously undescribed. The larva of this species fits nicely into the subgenus *Selfia*. The narrow mandible shape is a trait of the subgenus and similar to those of consubgenerics *Culicoides hieroglyphicus* Malloch and *Culicoides jacksoni* Atchley (Atchley 1970, Murphree and Mullen 1991). The presence of angular teeth on comb 4 would indicate placement in the *C. jacksoni* species complex (Atchley 1970). Measurements of field-collected larvae versus larvae that were reared in the laboratory were compared using a two-sample *t*-test. The field-collected larvae had significantly larger head lengths and widths ($t_5 = 4.71$, $P = .0053$). However, there were no significant differences in the head ratios ($t_5 = 0.48$, $P = .65$).

Subgenus *Selfia*
Culicoides jacksoni Atchley

Behavior and rearing.—A single female laid 85 eggs which hatched 5 days later. Larvae were seen feeding on *Pelodera* sp. nematodes.

Discussion.—The larva and pupa were previously described by Atchley (1970). This species was collected by Atchley in three, geographically disjunct, high elevation localities that represented its known distribution: New Mexico, northern Utah, and southern Arizona. This species was not immediately noticed in prior collections from southern California (e.g., Mullens and Dada 1992a) because females of most species of this subgenus cannot be identified to species (Atchley 1970). Only after males were recovered from a culture was it recognized as distinct from *C. brookmani*. The female was collected above 823 m, at the high end of the Deep Canyon site. This area lies below much higher adjacent coniferous forest (Toro Peak, elevation 2,657 m). This record represents a new locality for *C. jacksoni*.

Material studied.—Female, CO_2-baited trap, Riverside Co., CA., nr. Palm Desert 10-V-96.

Subgenus unplaced,
palmerae species group
Culicoides utahensis Fox
(Fig. 15)

Egg.—Cigar-shaped. Surface with symmetrical longitudinal rows of ansulae (Fig. 15A). Ansulae thickly stalked, expanded apically forming concave surface, lacking noticeable meshwork (Fig. 15B). Secondary small papillate ansulae occur between rows. In some eggs a thin layer of cement, that appears to crack and peel away during development, lies over many ansulae and across the rows. Average length = 303 ± 16, width = 54 ± 3 μ (n = 7).

Discussion.—The eggs of this species did not hatch in culture. Most eggs of *Culicoides* species hatch between 3 days and two weeks after oviposition. Parker (1950) found that the eggs of *Culicoides grisescens* Edwards took over 200 days to hatch. The eggs of *C. utahensis* never hatched in the laboratory although embryogenesis beneath the chorion could be observed. If the egg of this species overwinters, it is possible that low temperatures are needed to initiate further physiological development.

Discussion

The collection of host-seeking females, use of an artificial host, and a laboratory rearing system proved a successful means of associating immature stages with adults. The method has been used previously by Breidenbaugh and Mullens (1999) to describe all life-stages of two species of *Culicoides* from the same study area. This technique is advantageous in that the entire cohort from the isofemale is unquestionably conspecific but probably results in a nar-

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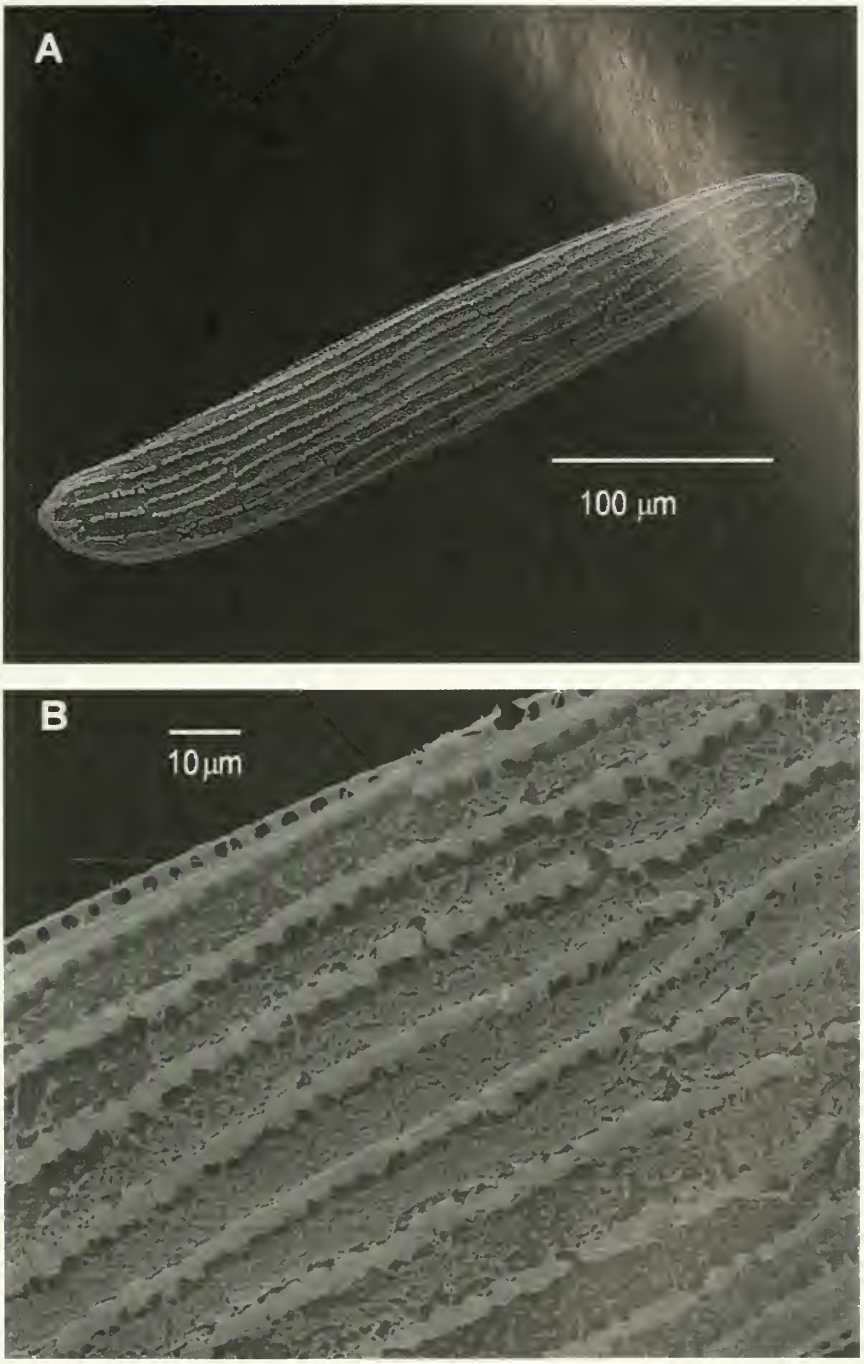

Fig. 15. *Culicoides utahensis*, egg. A) View of concave side of entire egg. B) Detail of egg surface.

rower range of measurements for morphometrical analysis than if field-collected material were examined. For example, field-collected larvae of *C. cacticola* and *C. brookmani* were found to have significantly longer head-capsules than laboratory-reared larvae. In the laboratory, an entire culture is not only genetically related but subject to similar nutritional parameters. Nevertheless, the morphological structures of laboratory-reared larvae are stable and a large series of all life-stages was generated without the tedium of multiple identifications or associations.

The rearing system of Petri dishes with an agar substrate was probably more effective in meeting the nutritional needs of predaceous species and less effective for facultative predators, herbivores, or detritovores. For instance, *Culicoides vetustus* Breidenbaugh and Mullens was never observed to feed on nematodes; this species also had the longest developmental time of any species reared (Breidenbaugh and Mullens 1999).

Eggs.—SEM is a valuable tool for describing *Culicoides* eggs (Kwan and Morrison 1974, Campbell and Kettle 1975, Nunamaker et al. 1987, Kariya et al. 1989, Day et al. 1997, Cribb and Chitra 1998, Breidenbaugh and Mullens 1999). Some authors have stated that specific patterns found on eggs can be helpful in species identification (Kariya et al. 1989, Cribb and Chitra 1998), and the variety of surface morphology shown in the present study supports this assertion. The eggs we encountered were separable based on length and width measurements in addition to unique surface structures.

Two types of ansulae were seen as surface structures on *Culicoides* eggs. Terms for these types are introduced: The longer, stalked structures with a meshwork surface, are called *ansulae elongata* and the shorter form, generally rounded and sometimes flattened into stripes, *ansulae papillae.*

Whether ansulae function in respiration or aid in adherence to the substrate has been widely debated. Within the Deep Creek drainage, substantial variations in ansulae form were found in species that develop along the stream margin. *Culicoides lahontan* has ansulae elongata, *Culicoides kettlei* Breidenbaugh and Mullens (Breidenbaugh and Mullens 1999) has ansulae papillae, and *C. brookmani* completely lacks ansulae. It is interesting to note that the egg of *C. cacticola* possesses ansulae papillae and is deposited on rotting cacti, a habitat which is less moist than stream margins. Experimental manipulations and studies of the eggs of a larger number of species might be helpful in ultimately determining the functional significance of the ansulae.

Larvae.—Characters employed by Murphree and Mullen (1991), for mostly eastern fauna, were found to be useful in describing and distinguishing between the larvae of *Culicoides* species found in southern California deserts.

Length of the head-capsule has often been used as a sorting tool (Jamnback 1965, Glukhova 1979, Murphree and Mullen 1991), but a strict reliance on length measurements could lead to misidentifications. In the present study, head-capsule length differed significantly between laboratory-reared and field-collected larvae (e.g., *C. cacticola* and *C. brookmani*), with the latter being larger. If reduced head-capsule length is the result of malnutrition, relatively smaller larvae may also be encountered in nature from adverse microhabitats. Seasonal temperatures also can influence size of mature larvae and subsequent adults (Linley and Hinds 1976). Since it is difficult to separate species without using size as a variable, it is suggested that morphological features be coupled with size whenever possible.

Variable success was encountered when using Murphree and Mullen's (1991) key to subgenera and species for larvae of North American *Culicoides* with measurements from the current study. Following their key, *C. freeborni* and *C. lahontan* missed the subgenus *Culicoides* due to the small head-

capsule lengths of our laboratory-reared specimens. However, *C. boydi* and *C. brookmani* correctly keyed to their respective subgenera, and *C. cacticola* correctly keyed to species using Murphree and Mullen (1991).

Pupae.—The greatest interspecific differences among pupae were seen in the respiratory horns and the opercula. The many somatic tubercles were also diagnostic but required detailed examination to recognize distinct differences between some species.

General comments.—The current subgeneric designations of *Culicoides* species (Wirth et al. 1985) are determined only on adult characters. Based on similar patterns in the immature stages, many of the groupings appear to be natural and, thus, the morphology of immature stages should be considered and included in phylogenetic interpretation of the genus *Culicoides*. For example, placement of adult females in the subgenus *Selfia* is based on the unique condition of unsclerotized spermathecae. The comparatively similar morphology of the larvae of this group also supports the subgenus as a natural group. Larvae possess a wide, rounded comb 4 on the epipharynx (combs 2 and 3 are lacking) (Atchley 1970, Murphree and Mullen 1991). The *Selfia* species studied here, *C. brookmani*, fits this description as well.

In another example, the pupae of the subgenus *Avaritia* have the opercular spines drawn out into elongate bristles (e.g., *C. chiopterus, C. boydi, C. obsoletus* (Meigen), *C. sanguisuga* (Coquillett)), a plausible synapomorphy for the group. Pupae of the subgenus *Culicoides* lack lateral spiracles on the respiratory horns.

Ansulae type may not be consistent among subgenera, however. For instance, ansulae elongata were found on eggs of two species in the subgenus *Culicoides* in this study (*C. freeborni, C. lahontan*), while Williams (1951) reported egg surface structures to be papillate in *C.* (*Culicoides*) *tristriatulus*. This trend is also displayed in the subgenus *Avaritia*. *Culicoides boydi* has obviously stalked structures on the egg surface, and Hill (1947) reports elongate structures on *C. obsoletus*; in contrast, micrographs of the egg of *C. sanguisuga* show ansulae papillae (Kwan and Morrison 1974).

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A NEW SPECIES OF RIPARIAN NABIDAE (HETEROPTERA) FROM THE HAWAIIAN ISLANDS

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Abstract.—A new species of Hawaiian Nabidae, ***Nabis gagneorum,*** is described from the islands of Maui and Molokai. This species is unusual among Nabidae in that it occurs in wet riparian habitats within and adjacent to swift streams. Figures of the male and female dorsal habitus and male paramere are provided, accompanied by a distribution map.

Key Words: Nabidae, riparian, Hawaiian Islands, Maui, Molokai

The damsel bugs in the genus *Nabis* have undergone a spectacular insular radiation in the Hawaiian Islands. Twenty-six endemic species are currently described from the islands (Zimmerman 1948), and an additional 27 new taxa are at hand in existing collections. As with many other Hawaiian insect radiations, the endemic Nabidae have diversified into a wide range of morphologically and ecologically divergent forms radically different from those seen elsewhere in the world. Among the most ecologically remarkable of these is a new riparian species, *N. gagneorum,* described below. This is the only riparian nabid so far documented, and its odd habits are yet another example of the unique adaptive shifts that often occur on isolated oceanic islands.

The presence of a riparian nabid in Hawaii was first brought to the attention of the author by the late Wayne Gagné during a visit to the Bishop Museum in 1986. Gagné had but a single specimen of this insect, and the brief nature of the visit did not allow a detailed analysis of its features. Following Gagné's untimely death in 1987, and a subsequent rehousing of the collection in a new compactor, the whereabouts of this specimen became obscure. In 1991, Frank Howarth, also of Bishop Museum, led the author to Iao Valley in the West Maui Mountains, the locality from which the original specimen had come, in an attempt to secure further collections. This foray was successful, and also allowed more detailed observation of this insect's unusual riparian habits. Once these latter were better understood and brought to the attention of collectors, it was possible to obtain additional specimens during the mid-1990's from various tributaries of Iao Valley, and from neighboring Olowalu and Honokohau valleys. Finally, in early 1997, a short series was taken from the East Fork of Kawela Gulch in the mountains of eastern Molokai, a surprising discovery indicating that the insect may be distributed in riparian habitats on all of the high volcanoes occupying the Maui Nui platform (i.e., West Maui, Haleakala, Molokai, and Lanai).

All measurements in the description below are given in millimeters. The holotype of *Nabis gagneorum* is deposited in the Bishop Museum, Honolulu, Hawaii (BPBM). Paratypes are deposited in that collection, at Cornell University, Ithaca,

New York (CUIC), and in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Nabis gagneorum Polhemus, new species
(Figs. 1–5)

Diagnosis.—A riparian species currently known from the West Maui Mountains (Fig. 4) and eastern Molokai (Fig. 5). Recognized by its dark coloration, semiaquatic habits, brachypterous wing form (Figs. 1, 3), and distinctive male parameres (Fig. 2).

Description.—*Brachypterous male:* Overall length 7.80, maximum width (across abdomen) 2.20; general appearance as in Fig. 1. General coloration of living specimens dark brown with a few scattered dark-yellow markings dorsally on head, thorax and hemelytra; legs paler than body, medium brown, becoming yellowish brown on basal segments; ventral body surfaces dark brown.

Head elongate, well produced both ahead of and behind eyes, length/width = 1.40/1.05, covered by a layer of short, pale, recumbent setae; width of vertex 1.50× the dorsal width of an eye (0.45/0.30); length of preocular portion of head 1.87× the dorsal length of an eye (0.75/0.40); length of postocular portion of head equal to 0.55× the dorsal length of an eye (0.25/0.40); ocelli well developed; length of antennal segments I–IV = 1.55/2.05/2.25/1.65; rostrum length 3.45, extending to bases of mesocoxae, lengths of segments I–IV = 0.35/1.30/1.30/0.50; coloration of head dark brown, with elongate yellowish patches along inner margins of eyes, tylus medium brown, elongate, shining; antennal segments I–IV uniformly yellowish brown except for single dark brown annulation near tip of segment II; eyes and ocelli red.

Pronotum trapezoidal, length/width = 1.65/1.67, covered by an obscure layer of very short, pale, recumbent setae; anterior collar well developed; anterior pronotal lobe weakly swollen and tumescent; posterior pronotal lobe short, not raised, posterior margin straight; overall pronotal coloration dark brown, with extreme posterior margin narrowly dark yellow.

Scutellum elongate and triangular, slightly raised at apex and to either side of midline basally, length/width = 0.57/0.60, covered with scattered short, pale, recumbent setae; coloration dark brown, often nearly black centrally, with a pair (1+1) of yellow spots to either side of midline on basal half.

Hemelytra elongate, submacropterous, extending to tip of abdomen, bearing scattered short, pale, recumbent setae; posterior margins acutely rounded, tips overlapping or very weakly divergent, membrane well developed, venation of corium and membrane well defined; coloration of corium dark brown with a few diffuse dark yellow maculations along veins, membrane leathery, fumate, with veins dark brown.

Legs elongate, with fore coxa approximately 2× as long as thick (0.75/0.45); fore femur fusiform, nearly 6× longer than wide (3.00/0.50), densely covered with short, pale, semi-recumbent setae; fore tibia slender, widening slightly at tip, inner margin bearing two parallel rows of 50–60 tiny black teeth bordered by pale, erect setae, outer margin bearing semi-erect pale setae; middle and hind femora, tibiae and tarsi slender, covered with short, pale, semi-erect setae; coloration of legs yellowish brown on tibiae and tarsi, all femora medium brown spotted with dark brown on distal sections, becoming yellowish brown at extreme bases, coxae and trochanters yellowish; all tibiae lacking dark annulations; lengths of leg segments as follows: fore femur/tibia/tarsomere 1/tarsomere 2/tarsomere 3 = 3.00/2.50/0.05/0.25/0.35; middle femur/tibia/tarsomere 1/tarsomere 2 = 2.90/2.75/0.10/0.30/0.37; hind femur/tibia/tarsomere 1/tarsomere 2 = 3.90/4.65/0.10/0.45/0.50.

Abdomen with extreme lateral portions of tergites III–VI exposed beyond lateral margins of hemelytra, lateral margins of these tergites broadly arcutate, segments VII and VIII narrowed, forming a box-like genital capsule, all tergites covered by an obscure

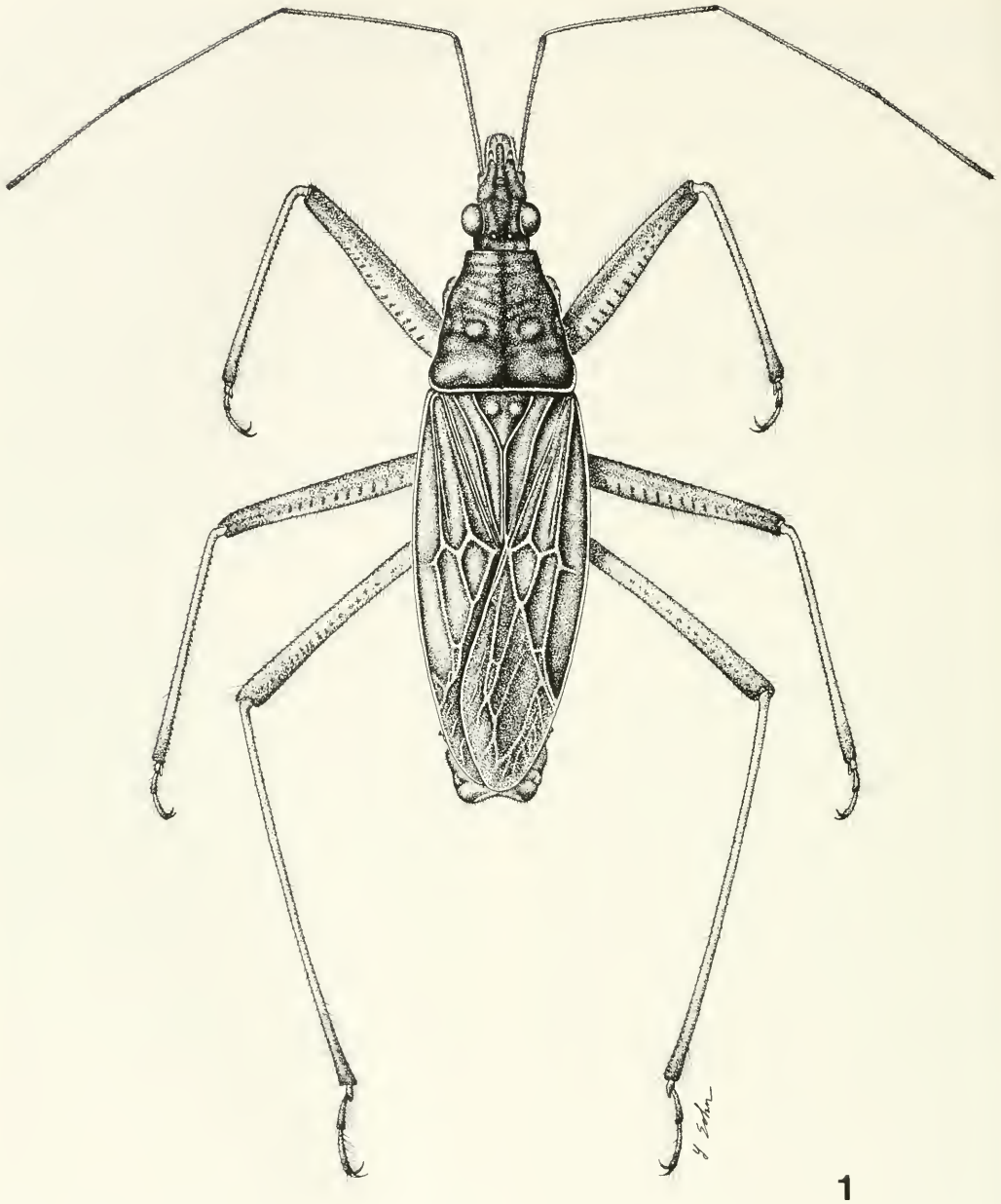


Fig. 1. *Nabis gagneorum,* male, shaded dorsal habitus.

layer of short, pale, recumbent setae; coloration of exposed tergites dark brown, with dark yellow markings at posterolateral angles.

Ventral surface dark brown, covered by short, pale, recumbent setae; round, dark yellow markings present around spiracles along abdominal paratergites I–VI, and irregular, transverse dark yellow patches present centrally along abdominal ventrites II–VI; tip of genital segment dark yellow.

Genitalia with basal section of paramere slender, distal section greatly expanded, ventral margin broadly arcuate, dorsal mar-

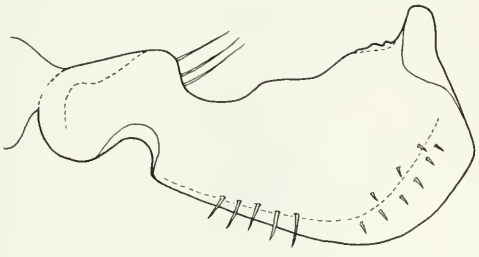


Fig. 2. *Nabis gagneorum,* male right paramere.

gin produced to a finger-like projection at tip (Fig. 2).

Brachypterous female: Length 8.30, maximum width (across abdomen) 2.90. Similar to brachypterous male in general structure and coloration but broader and more robust (Fig. 3); abdomen projecting laterally well beyond margins of hemelytra, exposing lateral portions of dark, shining-brown abdominal tergites and connexiva; abdomen also projecting posteriorly well beyond tips of hemelytra.

Etymology.—Named for Wayne and Betsy Gagné, whose combined efforts have done much to advance our knowledge of the remarkable Hawaiian Heteroptera biota.

Ecological associations.—Occurs on mossy rocks in and adjacent to swift mountain streams, and on wet bedrock walls bordering such streams.

Material examined.—Holotype, brachypterous ♂: HAWAIIAN ISLANDS, Maui, West Maui Mountains, Iao Valley, wet rock face above major stream junction [confluence of Nakalaloa and Poohahoahoa streams], 17 August 1991, CL 2563, J. T. and M. S. Polhemus (BPBM). Paratypes (all brachypterous): HAWAIIAN ISLANDS, Maui: 4 ♂, 1 ♀, same data as holotype (BPBM, USNM); 1 ♀, West Maui Mountains, Iao Valley, near lookout, 1 January 1973, F. G. Howarth, on rock near stream (BPBM); 1 ♀, West Maui Mountains, Iao Valley, 330 m. (1,000 ft.), on wet rock face above main Iao Stream, 16 August 1992, D. A. Polhemus (BPBM); 3 ♂, 2 ♀, West Maui Mountains, Iao Valley, along Ae Stream at head of Black Gorge, 365 m. (1,200 ft.), on wet rock face above stream, 17 May 1993, D. A. Polhemus (BPBM, USNM); 1 immature, West Maui Mountains, Olowalu Stream in upper Olowalu Valley, 365 m. (1,200 ft.), water temp. 19.5°C., 21 July 1994, 09:00–17:00 h, CL 8204, D. A. Polhemus (BPBM); 1 ♀, West Maui Mountains, Honokohau Stream, 395 m. (1,300 ft.), on boulders at streamside, 3 March 1998, H. Oppenheimer (USNM); 1 ♂, Molokai, East Fork Kawela Gulch at Puu Kolekole trail, TNCH Kamakou Preserve, Molokai Forest Reserve, 1,095 m. (3,600 ft.), 21°06′42″N, 156°54′26″W, water temp. 15°C., 28 May 1997, J. K. Liebherr (USNM); 1 ♀, 4 immatures, same locality as above but 31 May 1997, CL 8069, D. A. Polhemus (USNM).

Discussion.—Among the native Hawaiian Nabidae, *N. gagneorum* may be distinguished by its dark-brown coloration, submacropterous wing condition (Fig. 1), and distinctively shaped male paramere (Fig. 2). It is one of the few submacropterous Hawaiian nabids known to occur on more than a single island.

Nabis gagneorum is the first nabid to be discovered that is strictly confined to riparian habitats. At Black Gorge on Ae Stream, a tributary to Iao Valley in the West Maui Mountains, individuals were taken from vertical seeping rock faces adjacent to the stream, and on wet midstream rocks, with both adults and immatures found in these areas. Since *N. gagneorum* is a flightless species, the individuals discovered on midstream rocks must have arrived there by either passing through the stream waters, or by dispersing to these rocks at a lower stage of stream flow. The presence of immatures on the midstream rocks clearly indicated that the species was breeding there. Saldidae, which are the typical riparian Heteroptera in Hawaii (and elsewhere in the world), were also abundant at Black Gorge, but *N. gagneorum* was much larger in size than the largest saldid species present (*Saldula exulans* White), and thus appeared to

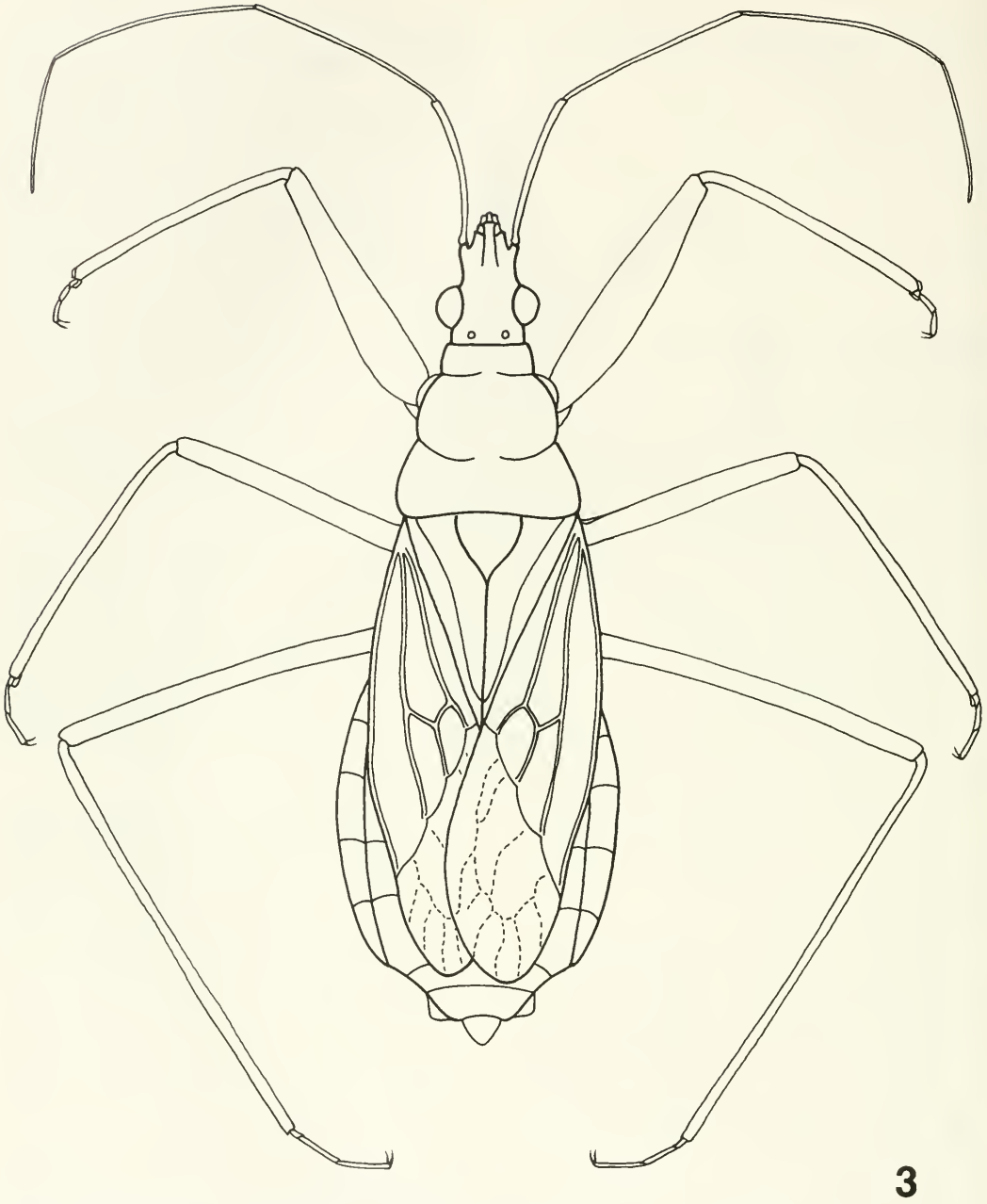
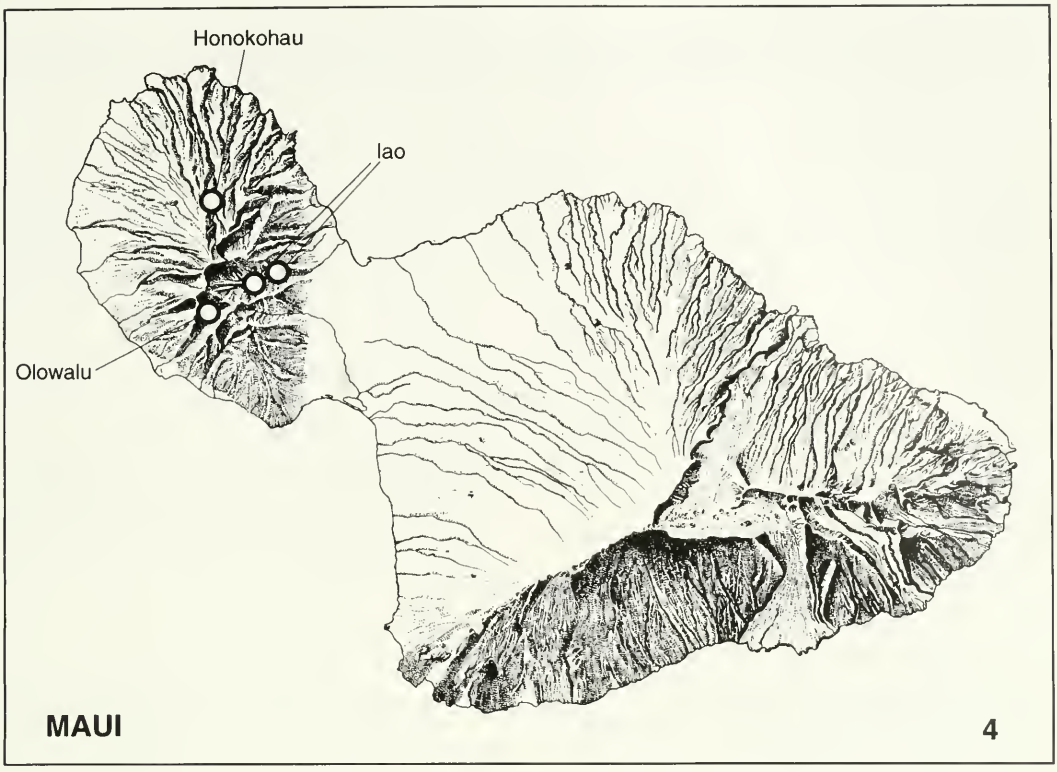
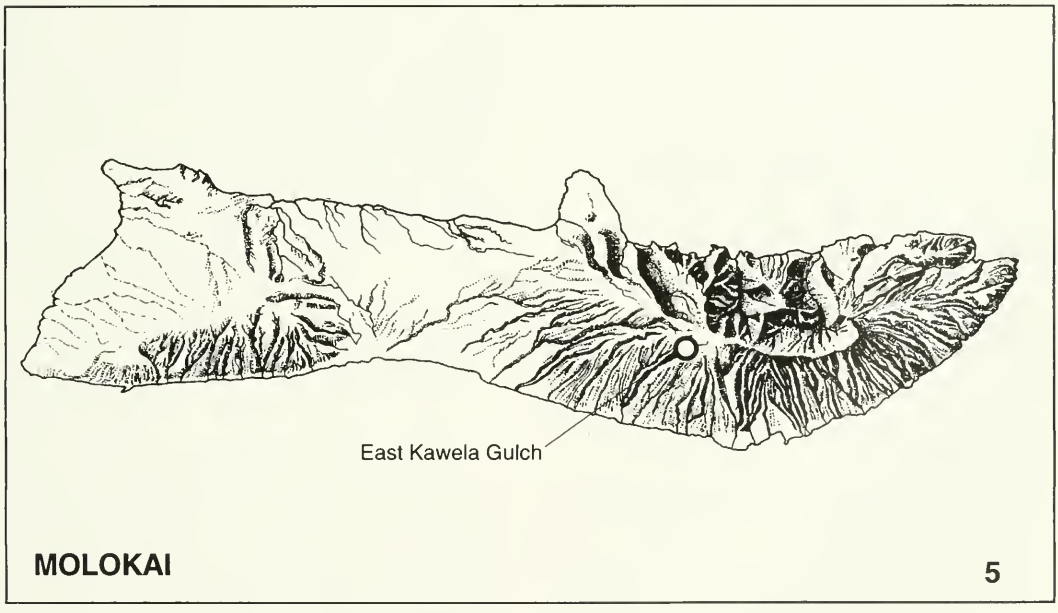


Fig. 3. *Nabis gagneorum*, female, dorsal habitus.

be occupying a slightly different riparian niche.

The series from Molokai was taken from moss covered rocks and bedrock exposures in the bed of the East Fork of Kawela Gulch just above the crossing of the Puu Kolekole trail. The first specimen taken, a male, was discovered while splashing the moss mats along the margin of a pool, in search of riparian Carabidae; subsequent specimens were obtained by lightly fogging these moss mats with a weak pyrethrin spray,





Figs. 4–5. Distribution of *Nabis gagneorum*. 4, Maui. 5, Molokai.

which caused the nabids to emerge from their hiding places. Visual searches and dismemberment of the moss mats in the absence of pyrethrin application proved useless, and demonstrated the ability of this species to elude detection by casual collectors using traditional techniques. Given this, it seems likely that diligent searches may produce additional collections of this species along other mossy streams on Molokai, the West Maui Mountains, and possibly Haleakala.

Acknowledgments

This project was initiated by the enthusiasm of Dr. Frank Howarth of the Bishop Museum, a steadfast champion for the conservation of Hawaiian insects, and sustained by the ceaseless energy of Betsy Gagné, of the Hawaii Natural Area Reserves System. I thank them both for their shared knowledge of *Nabis gagneorum* and its unusual habits. In addition, many of the collections reported on herein could never have been made without the assistance and companionship of Dr. James K. Liebherr, Cornell University and Curtis Ewing, University of Hawaii, during field surveys on Molokai and West Maui. Finally, thanks are due to Ed Misaki and Stefanie Loo of The Nature Conservancy of Hawaii (TNCH), who kindly provided access to the Kamakou Preserve on Molokai every time we asked, and to Bill Devick of the State of Hawaii Department of Land and Natural Resources, for funding stream insect surveys in Iao Valley.

I also wish to express my gratitude to Young T. Sohn of the Smithsonian Institution, who produced the excellent shaded habitus illustration.

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ADULT AMERICAN DOG TICKS (ACARI: IXODIDAE) AND CANINE-PRODUCED KAIROMONES

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Abstract.—In laboratory bioassays, adult American dog ticks, *Dermacentor variabilis* (Say), of both sexes became akinetic on residues from the hair from the flanks of dogs and from between dog's toes. When confined in petri dishes, female *D. variabilis* became akinetic on or above (on the lid) a canine paw print on a disc of filter paper. These findings help explain the distribution of host-seeking adult *D. variabilis* along trails.

Key Words: kairomone, arrestment, host-finding

The American dog tick, *Dermacentor variabilis* (Say), vector of Rocky Mountain spotted fever in the eastern U.S., is a three host tick. Its larvae and nymphs generally use small mammals as hosts and its adults feed on medium-sized or large mammals (Smith et al. 1946, Sonenshine et al. 1965). Even where common, larvae and nymphs of *D. variabilis* are rarely captured by dragging or flagging, whereas adults are easily picked up on drag cloths or on clothing (Sonenshine et al. 1965).

The propensity of adult *D. variabilis* to wait for hosts along animal trails has been recognized by several authors (Smith et al. 1946, Newhouse 1983, Carroll et al. 1991, Ginsberg 1992). The adaptive value to a tick of waiting along trails that are regularly used by host species instead of waiting at locations that are used little or not used at all by hosts is clear. Although *D. variabilis* can best be categorized as an ambushing type tick, Waladde and Rice (1982), Smith et al. (1946), Sonenshine et al. (1966), Carroll and Nichols (1986) and Carroll et al. (1991) demonstrated the ability of adult *D. variabilis* to disperse several meters. For instance, Carroll et al. (1991) recaptured marked adult *D. variabilis* along trails a few days after they had been released 8m from the trails. Attraction of adult *D. variabilis* of both sexes to host-produced kairomones was inferred by Smith et al. (1946) from a field experiment they conducted on Cape Cod, MA. Stakes and cloths that had been rubbed against the coats of dogs and urinated on by dogs were placed in an area infested with *D. variabilis*. Adult *D. variabilis* were subsequently observed on these treated stakes and cloths, but not on untreated stakes and cloths. It was unclear whether the urine or coat substances attracted and arrested the ticks.

In a laboratory study, Carroll (1999) found that substances rubbed from the dorsal surfaces of dogs' ears elicited an arrestment response (i.e., ceased ambulatory activity in response to a chemical stimulus) in adult lone star ticks, *Amblyomma americanum* (L.), blacklegged ticks, *Ixodes scapularis* Say and *D. variabilis*. The purposes of the present study were to discover whether adult *D. variabilis* responded only to kairomones from particular body regions of

dogs, and whether substances left on the substrate by a dog's feet act as *D. variabilis* arrestment kairomones.

Materials and Methods

Adult *D. variabilis* were collected in Prince George's and Queen Anne's Counties, Maryland, and maintained at 22°C, 95% RH and a photoperiod of 16:8 (L:D) h. Samples of canine coat substances were obtained by rubbing a clean glass rod (15 cm long, 0.5 cm diameter) against the flanks or between the toes of a dog's hind legs. The glass rods were handled only with clean vinyl gloves. The rods were placed in plastic bags according to body region and source animal and refrigerated at 3°C. Samples were taken from 6 different dogs belonging to several breeds (e.g., collie, pekingese, pit bull).

Samples of canine paw prints were obtained by pressing most or all of the plantar surface of a dog's hind paw on a disc of filter paper (Whatman No. 4, 15 cm diameter) marked into quadrants so that the paw only contacted one quadrant. The contacted quadrant was invariably detectable by smudges. Each paper was placed in a separate plastic bag and held at −15 °C until it was used in the bioassay.

Coat substance bioassay.—Ticks were released singly in the middle of small clay islands (2.5 by 1 by 1.3 cm). At one end of each island was a vertical glass rod that had been rubbed against the coat of a dog. At the opposite end of the island was a clean vertical glass rod that had been rubbed between the thumb and forefinger of a vinyl-gloved hand. Each clay island was centered in a plastic petri dish (3.5 cm diameter, 1 cm high) containing water. The petri dish was placed in a second, larger petri dish (10 cm diameter, 1.5 cm high) also containing water. The nested petri dishes containing the clay island were placed in a transparent Plexiglas glove box (65 by 85 by 45 cm) containing water ≈1 cm deep. The water prevented escape of the ticks and maintained high humidity (≈95% R.H.), favorable for the ticks, in the glove box. Tick location was recorded at 1, 18 and 24 h after a tick was released on a clay island. Between bioassays, clay islands were washed with soap and water, and thoroughly rinsed with water. Glass rods were similarly washed and rinsed, and also wiped with a tissue soaked with acetone and a tissue soaked in methanol.

Paw print bioassay.—A piece of filter paper with a paw print in one quadrant was placed in a glass petri dish (10 cm diameter, 1.5 cm high). A tick was placed on the centerpoint of the filter paper and the lid placed on the petri dish. To maintain high humidity in the petri dish, it was placed in a desiccator jar containing water below the rack. The location of the tick was recorded at 1, 18 and 24 h after it was released. Petri dishes were washed with soap and water, and rinsed with tap water between bioassays.

Data from the coat substance bioassays were analyzed by 2 × 2 chi square contingency tables. Tick responses to canine paw prints were analyzed as binomial samples using Fisher's exact test in StatXact (CYTEL) to determine if the response was the same for male and female dogs. Estimates and 95% confidence intervals for the probability of a tick responding to the treated paper (i.e., the tick found akinetic in the quadrant with the print) were calculated for each sex of dog.

Results

Adult *D. variabilis* of both sexes responded positively to substances rubbed from the flanks and from between the toes of dogs (Table 1). At 24 h after their release on clay islands with treated and untreated glass rods, 93.3% of female ticks and 86.7% of male ticks were on glass rods rubbed on dogs' flanks. All 30 female ticks tested and 90% of male ticks tested were on glass rods rubbed between dogs' toes 24 h after the tick's release on the clay island. Ticks responded similarly to substances rubbed from male and female dogs (Table 1).

Table 1. Number of ticks on glass rods rubbed on dogs and on untreated control rods at 24 h after ticks were released on clay island with the 2 glass rods. Thirty ticks of each sex were tested individually against samples from 3 male and 3 female dogs. Treatments and controls may total <30, because some ticks remained on the clay island or fell in the water moat.

		No. Ticks							
		Female Dog		Male Dog		Total of Dogs			
Samples	Sex of Ticks	Treatment	Control	Treatment	Control	Treatment	Control	X^2	*P*
Flank	Female	14	1	14	1	28	2	21.68	<0.0005
	Male	13	1	13	1	26	2	18.49	<0.0005
Toes	Female	15	0	15	0	30	0	28.36	<0.0005
	Male	14	1	13	1	27	2	20.03	<0.0005

In 18 of 25 trials, female *D. variabilis* were on or above (on the petri dish lid) the quadrant of the filter paper that had the paw print of a male dog ($P < 0.0001$) (Table 2). In contrast, only 10 of 25 female *D. variabilis* were on or above the paw prints of female dogs 24 h after the ticks were released in the petri dish. The 40% response of ticks to female paw prints was higher than the expected value of 25%, but it was nevertheless barely within the 95% confidence range of 0.21 to 0.61. Thus the ticks did not respond equally to paw prints from male and female dogs.

Discussion

The distribution of host-seeking adult *D. variabilis* within a given habitat is largely determined by the home ranges of their nymphal hosts, which are frequently small mammals, such as meadow voles, *Microtus pennsylvanicus* (Ord), and white-footed mice, *Peromyscus leucopus* (Rafinesque). Engorged nymphs may move short distances after they drop from their hosts. Because adult *D. variabilis* feed on medium-sized or large mammals, they may be ill-served by remaining at the spot where they metamorphosed from the nymphal stage. Host-seeking *D. variabilis* are capable of moving several meters over a period of days or weeks (Smith et al., 1946; Carroll et al. 1991). However, energy expended on locomotory activities unrelated to host or mate finding or survival (e.g., movement to a microhabitat with a more favorable relative humidity) is wasted. Although, micrometeorological factors (e.g., relative humidity, temperature) determine where host-seeking *D. variabilis* can wait for hosts (Harlan and Foster 1990, Rechav 1979), host-produced chemical cues, such as residues from canine hair and paw prints, further influence where adult *D. variabilis* wait for hosts. The locomotion required in finding a trail or area of host activity depletes a tick's energy reserves, but the expenditure is rewarded by the increased likelihood of contacting a suitable host.

Like a number of ixodids, adult *D. variabilis* are attracted to carbon dioxide sources (Carroll 1988). However, the attraction of *D. variabilis* to carbon dioxide does not adequately explain the occurrence of American dog ticks along trails. Carbon dioxide exhaled by passing animals may start ticks moving toward a trail, but such a source of carbon dioxide is transitory and will probably dissipate before the slow-moving ticks arrive at the trail. On the other hand, host-produced residues on vegetation or sub-

Table 2. Number of adult female *D. variabilis* on quadrant of filter paper with paw print of dog. Five ticks were tested against paw prints of each of 5 dogs (n = 25) for each sex of dog. Ticks on portion of lid of dish directly above quadrant with paw print were considered positive responses.

Female dogs			Male dogs		
No. ticks	%	*P*	No. Ticks	%	*P*
10	40	>0.05	18	72	<0.001

strate may provide a more lasting kairomonal cue. Such kairomonal residues may attract ticks or be contacted by dispersing ticks. The results of the paw print in bioassay showed that the residues from a single paw print can elicit an arrestant response in adult *D. variabilis*. The substrate of a regularly used animal trail may act as a figurative kairomonal magnet to host-seeking *D. variabilis* adults. Once at a trail, a tick is apt to encounter host-produced kairomonal residues on vegetation projecting into the trail. As the bioassays with canine coat substances showed, *D. variabilis* is likely to become akinetic on, above or near the vegetation contacted by hosts, if micrometeorological factors are favorable (Harlan and Foster 1990, Rechav et al. 1979).

Smith et al. (1946) reported the prevalence of adult *D. variabilis* along roads. They suspected that the ticks were attracted to the scent of dogs or people, that some component of automobile emissions might attract the ticks to roadsides, or that roads were barriers to tick dispersal. By marking ticks, they showed *D. variabilis* ticks tend to move to roads and will successfully cross them. Although frequent automobile use would create a gradient of combustion by-products along a road, and possibly have a factitious kairomonal influence on ticks in adjacent woods, the sensitivity of adult *D. variabilis* to canine-produced kairomones supports the host scent explanation for roadside tick distribution. If dogs tended to traverse open areas along roads rather than thickets, *D. variabilis* would also tend to be along the sides of the roads.

In the paw print bioassay, ticks responded with greater frequency to prints made by male dogs than to those made by females. However, because dogs of both sexes use the same trails, ticks drawn to or retained along trails by scents left by male dogs would also be picked up by female dogs. Other suitable host species also run the same trails during some of their activities.

In nature, it is not unusual to find two or more adult *D. variabilis* of the same or both sexes on the same twig or blade of grass. Host-produced kairomones may account for congregations of host-seeking *D. variabilis* at carrion (Kneidel 1984, Carroll and Grasela 1986) but pheromones may also play a role in clustering behavior.

These findings demonstrate the capacity of adult *D. variabilis* to perceive and respond to traces of kairomones rubbed from canine hosts. A paw print alone is sufficient to elicit an arrestant response. Most probably a well-used animal trail is readily recognized by *D. variabilis* adults, which in turn wait there for hosts. Further study is needed to determine the kairomonally active component in canine coat and paw substances, to elucidate any connection between tick responses to kairomones and production of pheromones, and to discover ways in which kairomonally mediated behavior can be manipulated (e.g., traps) to reduce the risk of tick bite and tick-borne diseases.

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QUEEN AND FORAGER SIZES OF *BOMBUS AFFINIS* CRESSON (HYMENOPTERA: APIDAE)

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Abstract.—This study explores the relationships of selected body measurements in the bumble bee *Bombus affinis,* and reviews the literature regarding measuring bumble bees. We found that in foraging workers of this species, collected over 3 sequential years from the same forest sites, compound-eye length, head length, head width, radial-cell length, scapus length, tibia length, and wing length all predicted dry weight, a measure of overall size. These same variables, except for head length, also predicted queen weight. Workers had a higher variance in their radial-cell length than queens, and queens had higher variances in their glossa length and weight than workers. In all 13 regression analyses between body size measurements, worker correlation coefficients (r^2 values) were higher than those for queens. Worker size, measured as head width (a strong predictor of body weight), increased with time during 2 out of 3 flight seasons.

Key Words: Apidae, bumble bee, forager size, seasonal size changes, queen size

Previous studies of *Bombus* size found that the relationships between linear measurements and between linear measurements and weights vary in strength depending on caste, sex, species, and measurement method (Knee and Medler 1965, Morse 1978, Harder 1985, and many references therein). This study on *B. affinis* Cresson examines samples of this bee from the same collection sites for 3 sequential flight seasons, documents many previously unreported intra-individual and forager-queen size relationships in the genus, and discovers an increase in forager size during its flight season.

Sizes of individual *Bombus* affect the pollination ecology of this genus which contains major pollinators in forests, meadows, tundras, and other habitats (Robinson and Johansen 1978). In some species, larger foragers fly faster, forage more efficiently on certain plants, gather more food during cool weather, obtain food from deeper flowers, and thieve less nectar than smaller foragers (Morse 1978, Pyke 1978, Heinrich 1979, Harder 1985). Because males and queens also vary in size within species (Owen 1989), and they are frequent flower visitors, they are also likely to have size-related effects on pollination; however, we found no published studies on this subject.

Bombus affinis is a short-tongued bumble bee, found from Ontario to New Brunswick and south to North Carolina (Mitchell 1962). It nests underground and flies from April through October (Laverty and Harder 1988). Wisconsin colonies commonly contain at least 200 workers, and can have up to 350 workers (Medler and Carney 1963).

Materials and Methods

We obtained a total of 475 foragers and 100 queens of *B. affinis* from 29 April through 27 September 1991–1993 with 20 Townes-style Malaise traps in four watersheds in the Fernow Experimental Forest, Tucker County, West Virginia (described in detail in Barrows et al. 1994, Barrows 1995). We emptied the traps every 10 days on the same Julian day of each year. The traps collected the bees in heads with 95% ethanol. We removed bees from alcoholic samples, air dried them for at least 1 yr, and randomly selected specimens for measurements. We then relaxed them in humidity chambers and dissected them to measure their parts.

Weight.—We took the weight-1 (W1) and weight-2 (W2) of each bee using an electronic balance (Mettler AE 50). Weight-1 was the weight of a bee's head, mesosoma, and metasoma; W2, the weight of only its head and mesosoma. We took W2s because food and organs within *Bombus* metasomas, e.g., crops, fat bodies, and ovaries, can cause their weights to vary appreciably (Alford 1969, Heinrich 1979). Because some specimens lost parts of their antennae, total antennae, and parts of their legs, we removed their entire antennae and legs distal to their trochanters to control for missing parts, before ascertaining their dry weights.

Linear measurements.—We measured left compound-eye length (CL), glossa length (GL), head length (HL), head width (HW), scapus length (SL), and tibia length (TL) using a dissecting microscope with an ocular grid, and we measured forewing lengths (WL1s, WL2s, and WL3s) with a microfiche reader (Minolta RP 605Z). Head width was measured as the greatest distance across a bee's compound eyes; HL, the distance from the vertex to the distal end of her clypeus; GL, the distance from the posterior end of her basiglossal sclerite to the tip of her labellum; WL1, her radial-cell length; WL2, distance from the proximal end of her median plate to the distal tip of her radial cell; and WL3, the maximum length of her entire forewing.

Before measuring glossae, tibiae, and wings, we straightened glossae by extending them into individual capillary tubes (Harder 1982), removed tibiae from their adjoining femora, and put detached forewings between microscope slides. We used glossae that were either relaxed in a humidity chamber or treated while still attached to their heads in a 10%-KOH solution for 12 hr at 25°C. Wing lengths were measured from images on a microfiche screen (Harder 1982, Owen 1988). Because 11 foragers and four queens had frayed wing tips, we did not attempt to measure their WL3s.

To investigate the change of forager size during the flight season, we measured head widths (HWs) of from one to eight specimens for each sampling period, using a maximum of eight bees when they were available. We measured HW because it is the linear measurement with the highest correlation with weight-2 (W2).

To discover possible correlations between sizes of body parts, we used least-square regression (SPSS for Windows, Norusis 1993). To look for possible differences between measurement variances, we used PROC TTEST (SAS Institute, Inc. 1979).

Results and Discussion

Queens of *B. affinis* showed a greater variation in measurement ranges than foraging workers in all measurements, except radial-cell length (WL1) and tibia length (TL) (Table 1). Further, queens had greater variances in glossa length (GL) and weight (W1 and W2) than workers, and the latter showed a greater variance in tibia length (TL) than the former (Table 2). Because queens are larger than workers, they would be expected to show greater variations and variances in all body-part sizes than workers. The possible biological significance of these three surprising exceptions to this expectation awaits discovery.

Workers showed significant correlations

Table 1. Measurements of *Bombus affinis*[a].

Measurement	Caste	N	Mean ± 1 SEM, Range (mg or mm)	Range Magnitude	Range Magnitude Queen > Worker
CL	queen	20	3.8 ± 0.03, 3.5–4.1	0.6	yes
	worker	20	2.7 ± 0.03, 2.6–3.0	0.4	—
GL	queen	20	6.4 ± 0.22, 5.4–8.4	3.0	yes
	worker	20	4.3 ± 0.08, 3.8–5.3	1.5	—
HL	queen	20	5.5 ± 0.05, 5.1–5.9	0.8	yes
	worker	20	3.8 ± 0.05, 3.5–4.2	0.7	—
HW	queen	20	5.8 ± 0.05, 5.1–6.1	1.0	yes
	worker	20	4.2 ± 0.04, 3.9–4.6	0.7	—
SL	queen	20	2.8 ± 0.03, 2.5–3.0	0.5	yes
	worker	20	2.0 ± 0.02, 1.9–2.3	0.4	—
TL	queen	20	6.7 ± 0.04, 6.5–7.1	0.6	no
	worker	20	4.7 ± 0.07, 4.2–5.3	0.9	—
W1	queen	20	185.8 ± 8.51, 129.7–258.8	129.1	yes
	worker	20	58.9 ± 3.25, 39.0–91.0	52.0	—
W2	queen	20	101.4 ± 3.56, 74.4–130.5	56.1	yes
	worker	20	34.1 ± 1.42, 24.0–48.3	24.3	—
WL1	queen	20	4.7 ± 0.04, 4.3–4.9	0.6	no
	worker	20	3.4 ± 0.05, 2.9–3.8	0.9	—
WL2	queen	20	14.8 ± 0.11, 13.9–15.5	1.6	yes
	worker	20	10.8 ± 0.15, 9.4–11.9	1.5	—
WL3	queen	16	18.3 ± 0.16, 17.2–19.2	2.0	yes
	worker	9	12.7 ± 0.18, 11.7–13.2	1.5	—

[a] All measurements are in mm, except for W1 and W2 which are in mg. CL, compound-eye length; GL, glossa length; HL, head length; HW, head width; SL, scapus length; TL, tibia length; W1, combined weight of head, mesosoma, and metasoma without legs and antennae; W2, weight of head and mesosoma without legs and antennae; WL1, length of radial cell of forewing; WL2, the distance from the proximal end of the median plate to the distal tip of the radial cell; WL3, the maximum length of the entire forewing.

($P \leq 0.05$) between all paired variables except for W2 and GL, and queens showed significant correlations between all paired variables except for this same pair and W2 and head length (HL) (Table 3). Worker r^2 values (which indicate the percent of the variability of the dependent variable explained by the independent variable) are higher than those for queens for all paired measurements. This suggests that natural selection has favored less variable body proportions in these foraging workers than in queens, and this is possibly related to greater behavioral specialization in foragers. They build brood cells, care for immatures, find and collect food, and work on and protect nests. Queens, which have greater behavioral versatility than workers, perform the above duties, and in addition, they search for hibernacula and nesting sites, hibernate, and mate.

Researchers have used different morphological features to estimate overall *Bombus* body size. Hobbs et al. (1961) measured their total body lengths, but considered them to be inaccurate reflections of size, due to the compressibility of metasomas. Medler (1962a), Knee and Medler (1965), Plowright and Jay (1968), Harder (1982) and Owen (1988, 1989) measured radial-cell lengths (WL1s). Plowright and Jay (1968) also used head width (HW) as a size indicator. Röseler and Röseler (1974), Morse (1977, 1978), and Harder (1982, 1985) measured wing lengths. However, only a few investigators examined the correlation of linear measures of body parts and weight. Harder (1985) found high, positive correlations between GL and body weight and between wing length and body weight in foragers and queens of seven *Bombus* spp., but he did not indicate exactly

Table 2. Comparisons of measurement variances of queens and workers in *Bombus affinis*[a].

CL	queen	0.014	worker > queen	0.8276
	worker	0.015		
GL	queen	0.745	queen > worker	0.0007[b]
	worker	0.115		
HL	queen	0.047	worker > queen	0.9304
	worker	0.049		
HW	queen	0.058	queen > worker	0.3475
	worker	0.038		
SL	queen	0.017	queen > worker	0.2065
	worker	0.010		
TL	queen	0.032	worker > queen	0.0310[b]
	worker	0.094		
W1	queen	1,447.829	queen > worker	0.0001[b]
	worker	211.223		
W2	queen	254.116	queen > worker	0.0001[b]
	worker	39.687		
WL1	queen	0.028	worker > queen	0.1678
	worker	0.053		
WL2	queen	0.218	worker > queen	0.1131
	worker	0.459		
WL3	queen	0.421	queen > worker	0.6130
	worker	0.292		

[a] Abbreviations are the same as in Table 1.
[b] $P \leq 0.05$. The null hypothesis is that the worker and queen variances are equal.

how he measured weight. Owen (1988) reported positive correlations between WL1 and body weight in *Bombus* queens of five of his eight investigated species. Neither researcher included *B. affinis*. We found that the highest morphological correlation between a weight and linear measurement in foragers is between W2 and HW ($r^2 = 0.74$) and in queens, between W2 and TL ($r^2 = 0.55$) (Table 3).

In our sample of 20 humidified *B. affinis* foragers, GL correlated with CL ($r^2 = 0.55$, $P = 0.001$), but not with HW ($r^2 = 0.31$), W2 ($r^2 = 0.20$), or WL1 ($r^2 = 0.24$). However, in our sample of 10 KOH-treated bees, GL and HW were correlated ($r^2 = 0.64$, $P = 0.006$), which indicates that the procedure used to relax dry specimens influences GLs.

Alpatov (1929) found the tongues of dry honey bees to be "about 6.5% shorter than the natural." Hobbs et al. (1961) stated that the GL of a dry bumble bee depends on whether it died with its tongue distended or contracted. Medler (1962b) investigated the correlation of different mouthparts to the WL1 for 14 *Bombus* species, and found them to be positively correlated, except in the queens of four species including *B. affinis*. Morse (1977) and Harder (1982) confirmed these results, and found even higher correlations for their samples, but did not investigate *B. affinis*. Waddington (1987) reported positive correlations between GL, HW, and WL1 in honey bees. Harder (1982) measured GL of specimens preserved in 70% ethanol and mentioned that a bee with its proboscis folded appears to have a shorter tongue than one with its proboscis extended. He suggested that the "sheath's compressibility and the freedom of the glossal rod from the sheath distally, which allows some of the rod to be drawn into the prementum during lapping and folding," accounts for this variability. We observed such GL differences macroscopically in *Bombus affinis*.

We found that W1 and W2 were correlated with one another in both queens and foragers of *B. affinis*. This indicates that

Table 3. Measurement regressions of *Bombus affinis*[a].

Regression	Caste	r^2	*P*	Regression Equation
W1 vs. W2	queen	0.81	0.0001[b]	W1 = −32.307 + 2.149 (W2)
	worker	0.88	0.0001[b]	W1 = −14.868 + 2.165 (W2)
W2 vs. CL	queen	0.25	0.0245[b]	W2 = −159.620 − 68.504 (CL)
	worker	0.68	0.0001[b]	W2 = −81.140 + 42.429 (CL)
W2 vs. GL	queen	0.01	0.7269	W2 = 89.801 + 1.947 (GL)
	worker	0.19	0.0800	W2 = 1.323 + 7.878 (GL)
W2 vs. HL	queen	0.17	0.0704	W2 = −67.295 + 30.419 (HL)
	worker	0.45	0.0011[b]	W2 = −38.360 + 19.221 (HL)
W2 vs. HW	queen	0.40	0.0030[b]	W2 = −140.141 + 41.534 (HW)
	worker	0.74	0.0001[b]	W2 = −83.866 + 28.001 (HW)
W2 vs. SL	queen	0.33	0.0085[b]	W2 = −95.292 + 69.129 (SL)
	worker	0.50	0.0005[b]	W2 = −57.711 + 45.402 (SL)
W2 vs. TL	queen	0.55	0.0004[b]	W2 = −320.748 + 62.512 (TL)
	worker	0.62	0.0001[b]	W2 = −42.532 + 16.175 (TL)
W2 vs. WL1	queen	0.32	0.0096[b]	W2 = −152.211 + 53.976 (WL1)
	worker	0.66	0.0001[b]	W2 = −42.036 + 22.301 (WL1)
W2 vs. WL2	queen	0.38	0.0038[b]	W2 = −211.339 + 21.043 (WL2)
	worker	0.69	0.0001[b]	W2 = −49.339 + 7.705 (WL2)
W2 vs. WL3	queen	0.46	0.0037[b]	W2 = −230.044 + 18.188 (WL3)
	worker	0.48	0.0384[b]	W2 = −52.032 − 6.552 (WL3)
WL1 vs. HW	queen	0.53	0.0003[b]	WL1 = 1.787 + 0.504 (HW)
	worker	0.70	0.0001[b]	WL1 = −0.783 + 0.996 (HW)
WL2 vs. WL1	queen	0.91	0.0001[b]	WL2 = 2.325 + 2.668 (WL1)
	worker	0.95	0.0001[b]	WL2 = 1.021 + 2.873 (WL1)
WL3 vs. WL1	queen	0.84	0.0001[b]	WL3 = −0.073 + 3.884 (WL1)
	worker	0.93	0.0001[b]	WL3 = 2.305 + 3.166 (WL1)

[a] The abbreviations are the same as in Table 1.
[b] $P \leq 0.05$.

dried objects in metasomas did not weigh enough to obscure these correlations under our study conditions.

Nonetheless, internal food, stored-fat, and ovarian development can affect a fresh bumble bee's overall weight. A bumble bee can become up to 100% heavier due to provisions in its honey crop found in its metasoma (Heinrich 1979). Researchers have measured fresh *Bombus* body weight, but they either ignored internal food (Pyke 1978), or tried to account for it by starving the bees for 12 to 18 h before weighing them (Harder 1983, 1985, Owen 1988). According to Alford (1969), fat makes up an average of 34% of the total dry weight of queens in autumn. Fat and glycogen are stored in the fat body, located in the metasoma. Holm (1972) reported an average fat content of 21% in the dry matter in the metasoma of autumn queens and 12% in spring ones. Because most of the queens investigated in our study were spring queens, fat may have made little contribution to their weight variability. Finally, ovarian developmental state contributes to the varying weight, especially in queens caught in spring (Cumber 1949).

In *B. affinis,* measurements of foraging worker HWs within a season indicate that forager size increased in 1992 ($r^2 = 0.93$; $P < 0.001$; N = 52) and 1993 ($r^2 = 0.61$; $P = 0.005$; N = 64), but not in 1991 ($r^2 = 0.02$; $P = 0.734$; N = 33) (Fig. 1). The small 1991 sample size possibly prevented our finding a forager size increase for that year.

Worker size might increase during flight seasons in many *Bombus* species. So far, quantitative studies have also documented

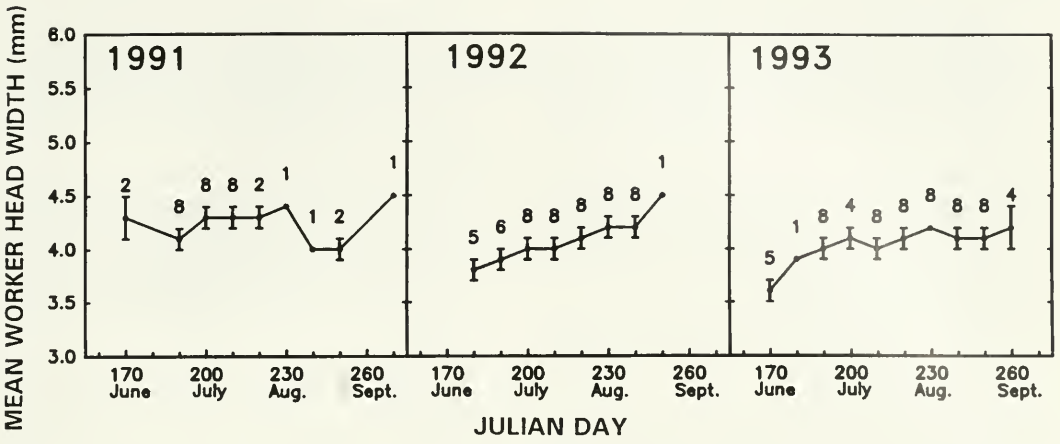

Fig. 1. Mean worker head width versus sampling period, Fernow Experimental Forest, WV, 1991–1993.

this increase in *B. fervidus* (Fabricius), *B. griseocollis* (De Geer), *B. nevadensis auricomus* (Robertson), and *B. perplexus* Cresson (Knee and Medler 1965, Plowright and Jay 1968). These increases occurred in healthy bumble-bee colonies, but the size of workers decreased when colonies were parasitized (Knee and Medler 1965). Our samples from Malaise traps may have contained bees from both healthy and parasitized colonies, and colonies in different developmental stages, which might have lowered our size-season correlation coefficients.

In conclusion, we found that many body measurements are significantly correlated with body weight and other body measurements in both queens and foraging workers of *B. affinis*. Tibia length is most correlated with weight in queens, and head width is most correlated with weight in workers. Radial-cell length is highly correlated with total wing length in both castes. Laboratory-preparation methods influenced glossa length, and, therefore, whether it correlated with other body parts in our study. Forager size increased during the flight season in 2 out of 3 yr. Our results and literature review suggest that researchers should measure other *Bombus* species from different habitats to obtain a more complete understanding of *Bombus* size. Further, the relationships of queen and worker size with competitive interactions involving conspecific bees and other animals at flowers, foraging efficiency, frequency of flower robbing and thieving, kinds of flowers used, and other phenomena still remain unstudied, or only meagerly studied, in most *Bombus* species.

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DESCRIPTIONS OF THE FINAL INSTAR LARVAE OF *ARGIA SABINO* GARRISON AND *ARGIA PIMA* GARRISON (ODONATA: COENAGRIONIDAE)

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Abstract.—We illustrate and describe the final instar larvae of *Argia sabino* Garrison 1994 and *Argia pima* Garrison 1994 based on preserved exuviae and larvae from Sabino Creek, Arizona, U.S.A. A dichotomous key is provided to integrate *A. sabino* and *A. pima* into an existing larval key to North American *Argia spp.*

Key Words: Arizona, damselflies, Zygoptera, larval taxonomy, *Argia*

Argia sabino Garrison is a species of conservation concern because of its limited range and possible endemism. The species is known from only three localities globally and from only one U.S. breeding population at Sabino Creek, Arizona (Garrison 1994). *Argia pima* Garrison is closely related to *A. sabino* and the two species are sympatric at Sabino Creek. Here we describe the final instar larvae of both species. This project was undertaken in support of studies on the habitat requirements of *A. sabino.*

Argia is a diverse odonate genus, containing about 110 species (Garrison 1994). The larvae of the genus are poorly known. Of 36 North American *Argia spp.*, Westfall and May (1996) provide a key to identify the larvae of 29 species. Larvae of only 28 *Argia spp.* have been formally described (Novelo-Guiterrez 1992). Continued progress in describing larvae will benefit our understanding of the evolution and systematics of the group. In addition, development of comprehensive larval keys to *Argia* will facilitate ecological studies of benthic invertebrates in many habitats. Frequently, several species of *Argia* are sympatric in small streams, particularly in the southwestern U.S. and southward into the Neotropics. For example, eleven *Argia* species are known from Sabino Canyon (R.W. Garrison, personal communication). At any given time or location, up to eight of the Sabino Canyon species may be common or quite abundant (personal observation).

Our descriptions include a treatment of the male and female gonapophyses, which Novelo-Guiterrez (1992) showed to be highly diverse and taxonomically useful structures within the genus. We also provide a diagnosis of the larvae, and integrate the two species into Westfall and May's (1996) key to North American *Argia* larvae.

METHODS AND MATERIALS

Argia larvae in all stages of development were collected from Sabino Creek, Arizona, U.S.A. in May 1996 and from March to July 1997. Collections were made with a standard D-frame aquatic collecting net from shallow areas of pools, primarily by lifting or turning rocks and scooping up dislodged substrate and invertebrates. The net was also swept among submerged root mas-

ses and leaf litter. *Argia* larvae were maintained at 20°C on a 14:10 (L:D) cycle in 120 ml plastic specimen containers that were supplied with a strip of cordura nylon webbing as a clinging substrate. Larvae were fed mosquito larvae, *Daphnia,* ostracods, and tubificid worms *ad libitum* (late-instars were primarily fed tubificid worms) until they emerged. Final stadia ceased feeding when emergence was imminent. At this time, each larval container was provided with an emergence stick and placed in an emergence chamber (inverted 3.8-liter glass condiment jar) to contain the imago. All exuviae and some larvae were preserved in 80% EtOH. Teneral adults were allowed to harden until they could be identified and then were preserved in 80% EtOH with the associated larval exuviae. We measured exuviae and larvae with a Lasico model S-4 auto-scaler. Illustrations were prepared with a camera lucida at 12× (dorsal habitus), 25× (prementum and lamella), and 50× (gonapophyses) magnification.

Descriptions

Argia sabino Garrison 1994
(Figs. 1–5)

Final instar larva.—Robust; ground coloration pale to medium brown; markings deep brown to black. Measurements presented in Table 1. *Head:* Dorsum of head patterned as shown (Fig. 1). Ocelli visible as white semicircular depressions. Cephalic lobes with dorsum irregularly patterned; posterolateral margins of lobes broadly angulate, darkly pigmented, and with a fringe of stout setae. Antenna 7-segmented; scape broad, short with apical fringe of fine setae; pedicel longer, broad with rounded apex; remaining segments elongate. All segments light brown. Antennomere lengths (from basal to distal) approximately as 0.4: 0.7: 1.0: 0.9: 0.5: 0.3: 0.1. Labium pale to medium brown. Prementum (Fig. 2a) with stout setae along distal 0.4 of lateral margins, a cluster of 3–8 basidorsal stout setae, and a series of 3–7 fine, short dorsoapical setae; basidorsal and dorsoapical setae sometimes absent. Ligula strongly to moderately prominent, with closely set minute claviform setae along margin. Premental palpus with 3 (sometimes 2) long dorsal hairlike setae; dorsal movable hook (brown) and pair of ventral hooks present; the ventral pair longer than dorsal hook and tinged with brown. *Thorax:* Pronotum with scattered stout setae and usually a pair of dorsal spots. Lateral pronotal margins produced with clump of stout setae. Synthorax relatively dark with obscure patterning. Wing sheaths with dark bands as shown in Fig. 1; tips of posterior pair typically extend to the posterior margin of abdominal tergite 4. Sternites unpigmented with scattered fine setae and a single long fine seta anteromesal to each mesocoxa. Femora with 2 dark transverse bands each, the distal band larger; bands narrower than intervening spaces. Profemur with regularly spaced stout setae along posterior, anterior, dorsal, and ventral margins; stout setae fewer in similar positions on meso- and metafemora. Tibiae with dark transverse band slightly basal to center and usually with dark area near articulation with femora. Tarsi 3-segmented, light brown, with pair of strongly curved claws. Tibiae and tarsi with thick dorsal growth of long fine setae. Stout setae along ventral margin of tibiae; setae increasing in extent and number to form dense patch near apices. Several setae near apices trifurcate, comblike. Ventrally directed, finer stout setae present in two rows along ventrolateral edges of tarsi. *Abdomen (excl. appendages):* Abdominal tergites 1 and 2 usually unpatterned; 3 and 4 variable, often with irregular dark patterns; 5–7 with dorsolateral and lateral dark blotches paired about dorsal midline, these blotches continuous with posterior margin and tapering anteriorly in tergum 7; 8 and 9 primarily deep brown with light areas centered on midline and tapering abruptly to thin line posteriorly; 10 notched with lateral faces dark and broad

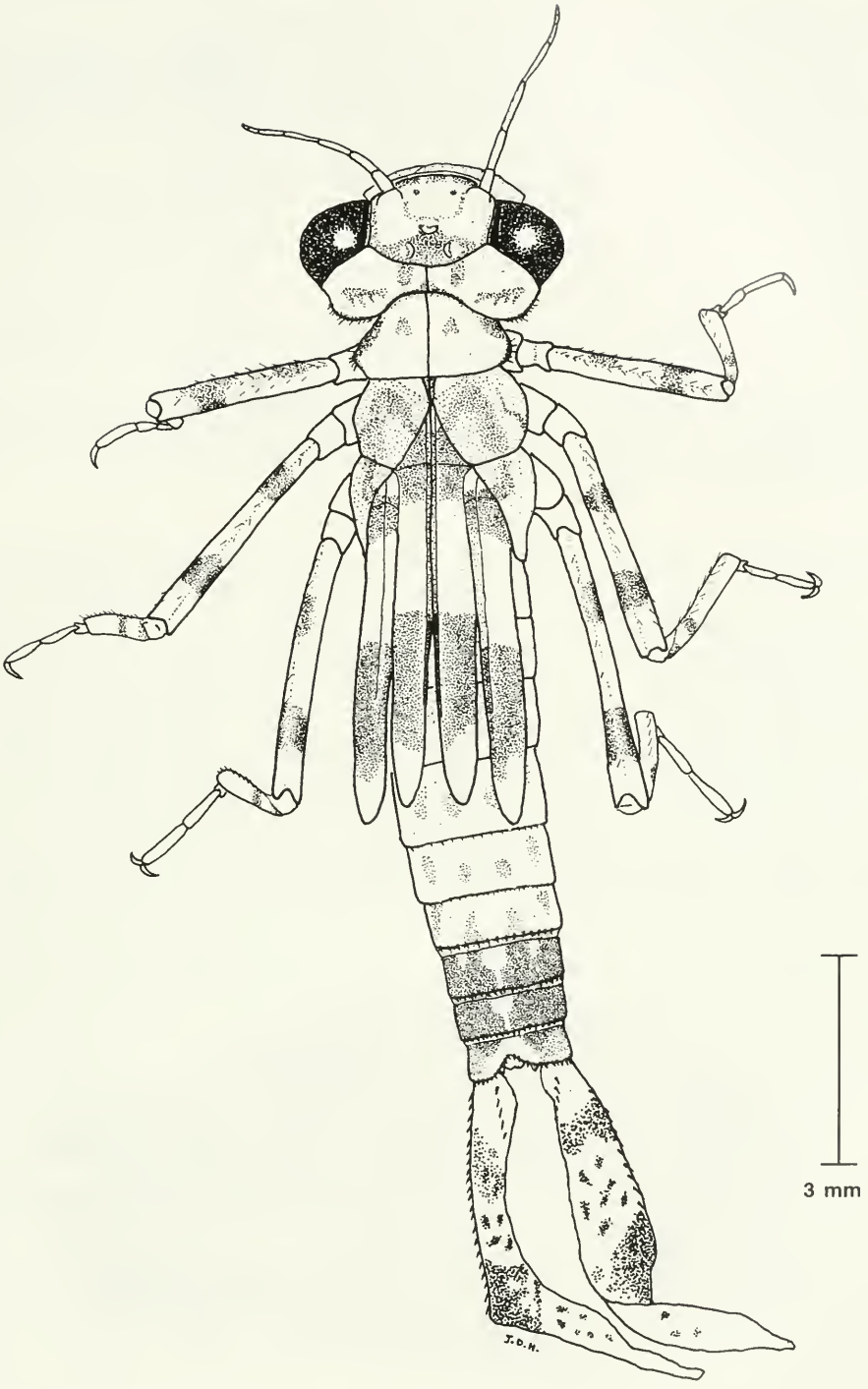


Fig. 1. Dorsal habitus of final instar larva, *Argia sabino.*

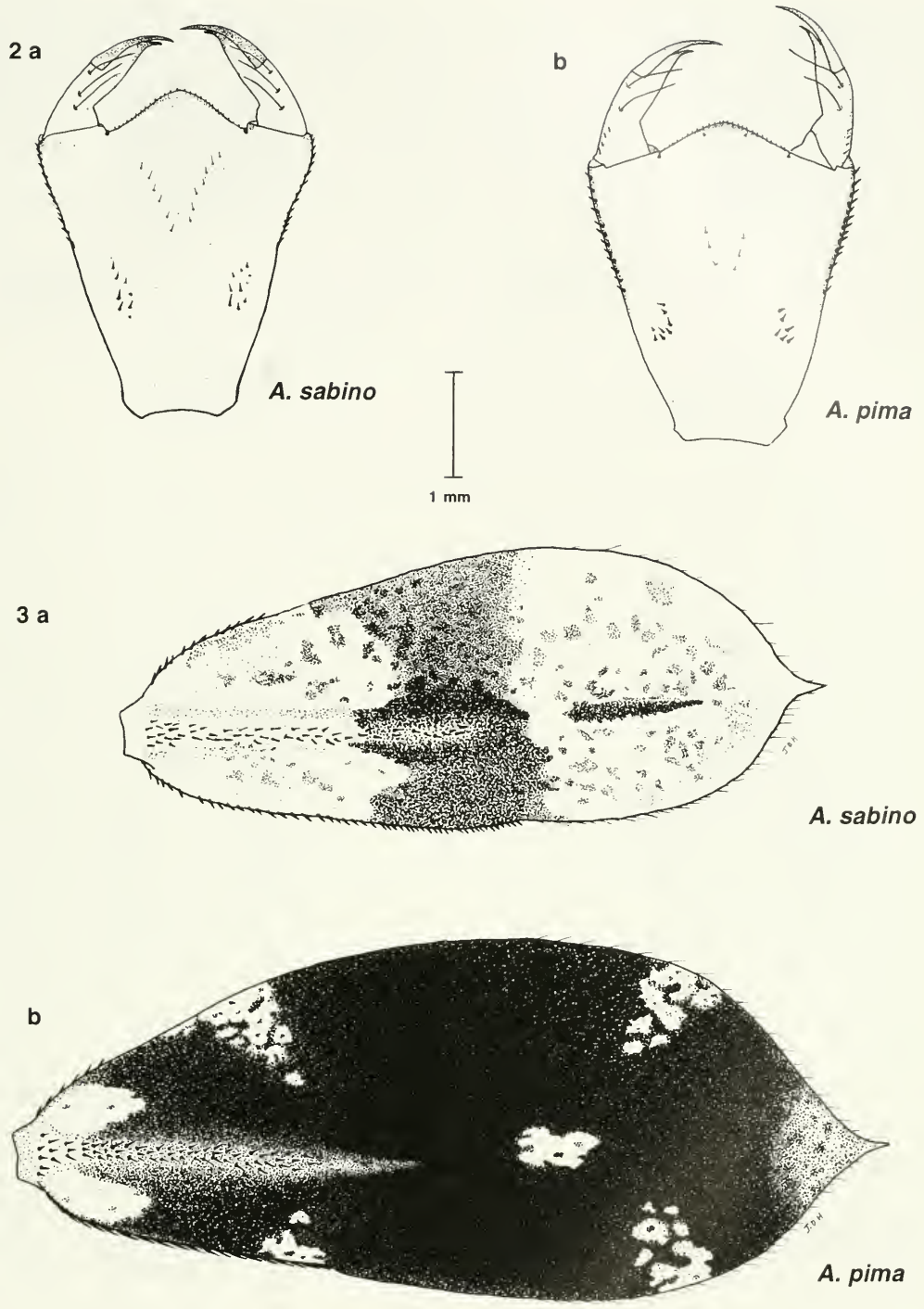
Table 1. Measurements* of final instar larvae, *Argia sabino* and *Argia pima*.

	Head Width	Total Length	Hind Femur Length	Hind Wingpad Length	Lateral Lamella Length
Argia sabino					
Males (n = 5):	3.4–4.0	11.7–15.2	3.7–4.2	3.9–5.0	
	(3.7 ± .23)	(13.1 ± 1.4)	(4.0 ± .25)	(4.5 ± .55)	5.4–6.5
Females (n = 9):	3.4–3.8	11.1–16.4	3.6–4.3	4.3–5.0	(6.0 ± .23; n = 8)
	(3.6 ± .08)	(13.9 ± 1.1)	(4.1 ± .15)	(4.7 ± .12)	
Argia pima					
Males (n = 7):	3.9–4.1	12.7–17.7	4.0–4.5	4.4–4.8	
	(4.0 ± .06)	(14.8 ± 1.47)	(4.2 ± .25)	(4.6 ± .08)	6.2–7.8
Females (n = 8):	3.9–4.1	12.7–16.9	4.2–4.6	4.6–5.2	(7.0 ± .40; n = 7)
	(4.0 ± .06)	(14.7 ± 1.22)	(4.4 ± .11)	(4.9 ± .15)	

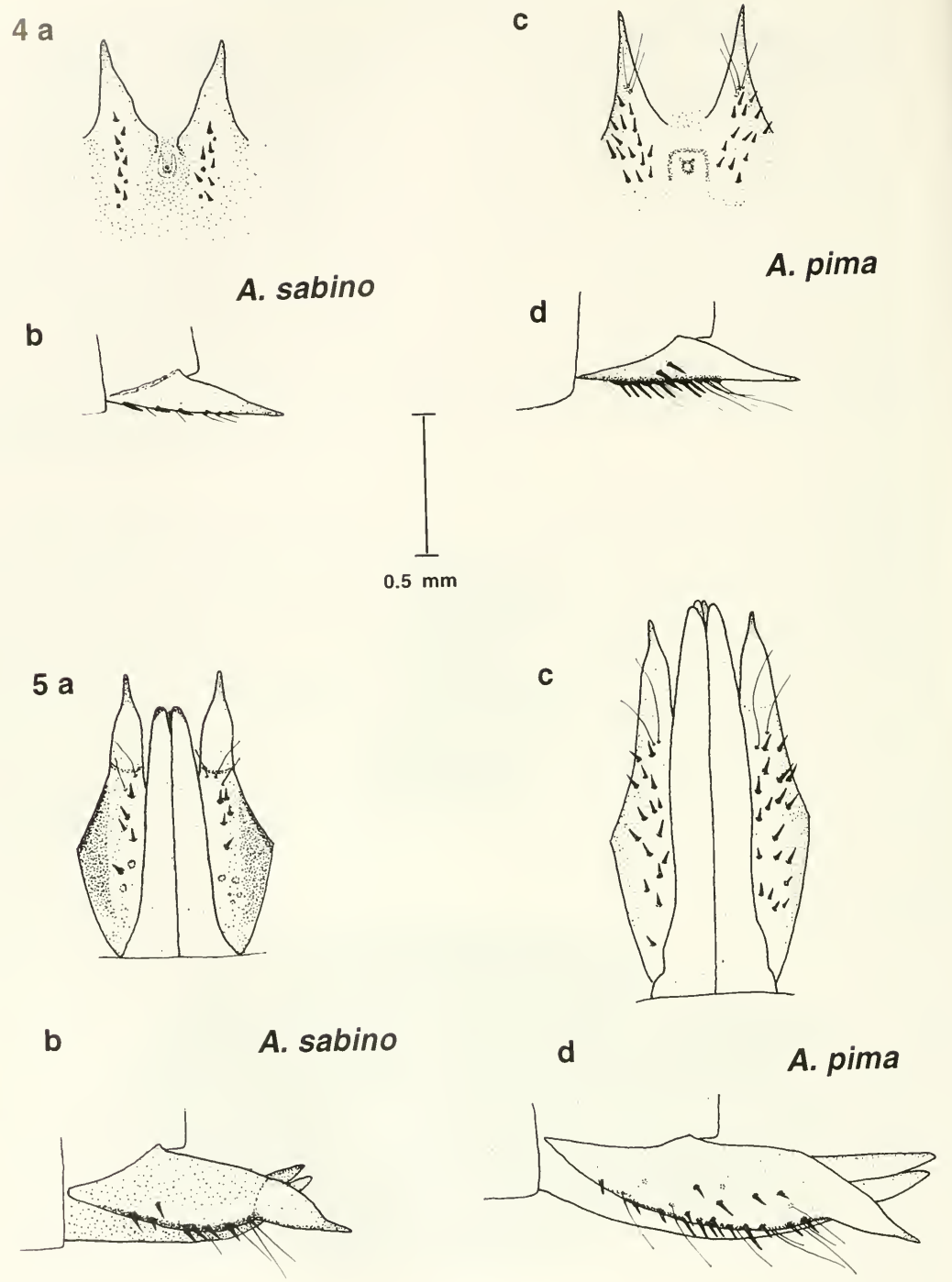
* Range in mm; mean ± 90% confidence half-interval in parentheses. Measurements for lateral caudal lamella length not reported by sex. Total length excludes caudal lamellae. Not all specimens examined were measured because some were damaged or distorted.

pale area centered on dorsal midline. Tergites 1–4 clothed with long fine setae, without stout setae; 5–10 with fewer fine setae and increasing densities of stout setae; stout setae particularly prominent along posterior margins of 8–10. Lateral pleura of segments 3–10 with stout setae increasing in size and density on posterior segments. Sternites 1–6 unpigmented with sparse fine setae; 7–10 progressively darker with increasing densities of stout setae especially along posterior margins. *Caudal lamellae:* Caudal lamellae laminar (slightly inflated basally) with moderately accuminate tips. Lateral lamellae (Fig. 3a) 2.5 times as long as wide with lateral external carinae extending along basal 0.5 of length of lamella and bearing stout setae; stout setae present along basal 0.1 and 0.6 of dorsal and ventral margins, respectively. Median caudal lamella less than twice as long as wide and without lateral carina; analogous central lamellal keel without stout setae. Median lamella with stout setae along basal 0.4 and <0.1 of length of dorsal and ventral margins. Lateral lamella largely pale with scattered dark spots or mottling except for black transverse band covering mesal ¼–⅓ of lamella, centered on terminus of lateral carina. Band darkest ventrally, fading to a broken area of dark spots dorsally in some specimens. Median caudal lamella with central transverse band less prominent than in lateral lamellae, and usually with more extensive mottling on distal and basal ends of gill. *Gonapophyses and cercus:* Male gonapophyses (Figs. 4a, b) light brown, pyramidal to elongate, with acute tips parallel and extending to posterior 0.4 of sternite 10. Basal 0.6 of venter of gonapophyses with series of 4–8 principal and a few smaller stout setae directed posteriorly and closely appressed; a few fine setae also present. Male cercus without prominent distal points; inner margin convex in dorsal view; distance between cerci in dorsal view less than or equal to their maximum width. Female gonapophyses (Figs. 5a, b) with acute tips of outer pair parallel to slightly divergent and extending to posterior 0.8 of tergum 10. Tips of inner pair extend to posterior 0.8 of outer pair in ventral view. Basal 0.7 of venter of outer pair with series of 5–10 principal and several smaller stout setae; fine setae also present.

Remarks.—Characters relating to relative extensions of structures (e.g. extension of wing sheaths relative to abdominal tergite 4) are variable due to differences in posture and extension of preserved specimens. Body patterns may be obscure in very dark or pale individuals; pigmentation patterns are much more distinct in preserved larvae than in exuviae. The above description is



Figs. 2–3. Labium and lateral lamella. 2, Prementum, dorsal view; a, *Argia sabino,* b, *A. pima.* 3, Left lateral lamella, lateral view; a, *A. sabino,* b, *A. pima.*



Figs. 4–5. Gonapophyses. 4, Male gonapophyses in ventral (a, c) and lateral (b, d) view; a, b, *Argia sabino*, c, d, *A. pima*. 5, Female gonapophyses in ventral (a, c) and lateral (b, d) view; a, b, *A. sabino*, c, d, *A. pima*.

based on the following specimens: U.S.A., Arizona, Pima County, Santa Catalina Mts., Sabino Creek, under stones and in detritus in pools. Collected at 990–1,190 m on various dates, IV-10-97–VII-10-97. Exuviae: 3 males, 4 females, Florida State Collection of Arthropods, International Odonata Research Institute (FSCA/IORI); 2 males, 3 females, University of Arizona Insect Collection (UAIC). Larvae: 1 male, 3 females, FSCA/IORI; 1 male, 2 females, UAIC.

Argia pima Garrison 1994
(Figs. 2–6)

Final instar larva.—Similar in overall habitus to *A. sabino* but larger (Table 1) and slightly more elongate; ground coloration usually darker than in *A. sabino,* medium brown; markings deep brown to black (Fig. 6). *Head:* Patterns on dorsum of head similar to those in *A. sabino,* but less distinct. Ocelli, antenna, overall shape of head, and setation and shape of cephalic lobes as in *A. sabino.* Antennomere lengths approximately as 0.4: 0.7: 1.0: 0.8: 0.6: 0.2: 0.15. Labium pale to light brown; prementum (Fig. 2b) with stout setae along distal 0.5 of lateral margins, a cluster of 6–10 basidorsal stout setae, and usually with 1–3 dorsoapical fine setae; these less prominent than in *A. sabino.* Ligula moderately prominent; minute claviform setae set along apical margin; an additional pair of minute claviform setae also present, recessed from margin of ligula. Premental palpi usually with 2 hairlike setae, rarely with 3 on one palpus; palpal hooks as in *A. sabino. Thorax:* Pronotum with scattered stout setae but lacking pair of dorsal spots. Lateral pronotal margins with prominent knob covered with stout setae. Synthorax and wing pad patterns as in *A. sabino*; tips of posterior pair of wing pads typically extend to posterior margin of abdominal tergite 3. Sternites pale with scattered fine setae. Pigmentation and setation patterns of legs as in *A. sabino,* except dark areas on tibiae near articulation with femora usually more extensive and distinct. *Abdomen (excl. appendages):* Setation of abdominal tergites as in *A. sabino.* Abdominal color pattern similar to that of *A. sabino,* except white areas on dorsum of tergites 8 and 9 not narrowing posteriorly. Abdominal tergites 1 and 2 mostly pale; 3–5 with dark lateral areas and a paler bilobed marking centered on dorsal midline; 6–7 with dorsolateral and lateral dark blotches paired about dorsal midline, these blotches often continuous with posterior margin and tapering anteriorly on 7; 8 and 9 primarily deep brown with light stripe centered on midline; 10 notched with lateral faces dark and broad pale area centered on dorsal midline, this pale dorsal stripe widening posteriorly. Stout setae present along lateral pleura of segments 3–10. Setation and coloration of sternites as in *A. sabino* except stout setae less robust and abundant, especially on 8. *Caudal lamellae:* Caudal lamellae saccoid-laminar, basally inflated to a greater degree than in *A. sabino,* with moderately accuminate tips. Lateral lamellae (Fig. 3b) 2.5 times as long as wide with lateral external carinae extending along basal 0.4 of length of lamella and bearing stout setae; stout setae present along the basal 0.1 and 0.4 of dorsal and ventral margins, respectively. Median caudal lamella without lateral carinae; analogous lengthwise keel with a few stout setae near base of gill; stout setae along basal 0.2 and 0.15 of dorsal and ventral margins. Lateral lamellae largely velvety black; with light areas at basal 1/10 and a small pale spot roughly at center of gill; distal dorsal and ventral edges of gill often with mottled, wedge-shaped areas converging on pale central spot (Fig. 3b). In some individuals, mottled areas nearly reach central spot. Median caudal lamella similar in pigmentation to lateral lamellae, but with markings more diffuse and with light areas more extensive than in lateral lamellae. *Gonapophyses and cercus:* Male gonapophyses (Figs. 4c, d) light brown, more elongate than those of *A. sabino,* with acute tips parallel and extending to posterior 0.4 of tergum 10. Basal 0.7 of venter

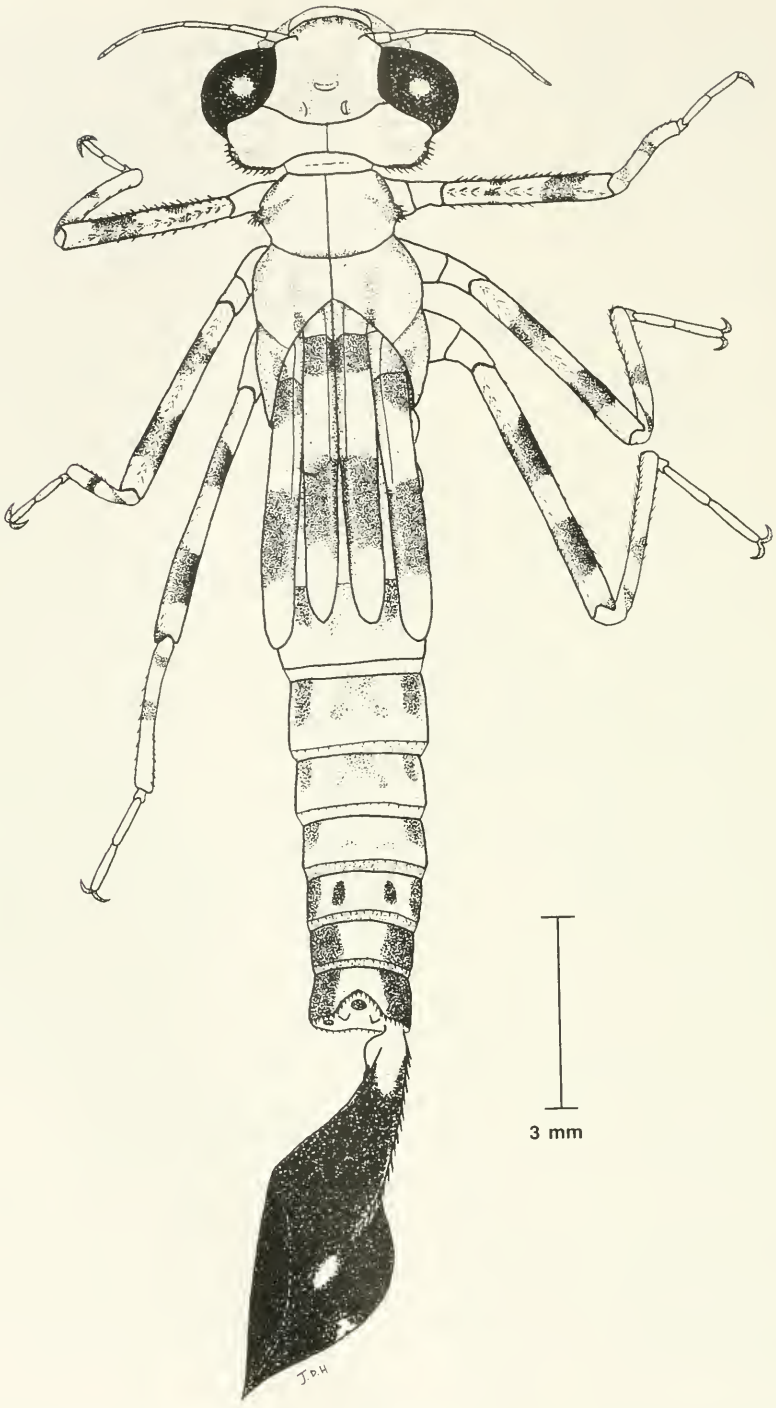


Fig. 6. Dorsal habitus of final instar larva, *Argia pima*.

of gonapophyses with series of 10–15 principal and several smaller stout setae directed posteroventrally; 2–4 fine setae also present. Male cercus as in *A. sabino,* except distance between cerci in dorsal view usually greater than their maximum width. Female gonapophyses (Figs. 5c, d) with acute tips of outer pair slightly divergent and extending beyond end of tergum 10. Tips of inner pair extend to or beyond tips of outer pair in ventral view. Basal 0.8 of venter of outer pair with series of 15–20 principal and several smaller stout setae; 6 principal and several smaller fine setae also present.

Remarks.—Variability noted for *A. sabino* also exists in *A. pima.* In particular, extension of abdominal segments may be extreme in specimens preserved *post mortem.* Some individuals are very darkly pigmented. The above description is based on the following specimens: U.S.A., Arizona, Pima County, Santa Catalina Mts., Sabino Creek, under stones and in detritus in pools. Collected at 1,100–1,190 m on VI-6-96 and on various dates, III-17-97–VII-10-97. Exuviae: 3 males, 4 females, FSCA/IORI; 2 males, 2 females, UAIC. Larvae: 1 male, 4 females, FSCA/IORI, 4 females, UAIC.

Diagnosis

Larvae of *A. sabino* and *A. pima* could not be integrated into the larval key of North American *Argia* (Westfall and May 1996) without modifying couplet 16 and subsequent couplets. We restructured the key, based on published information, to accommodate *A. sabino* and *A. pima.* The key below is valuable primarily in determining specimens collected from southern Arizona and Mexico. All figures referred to are contained in this publication.

Key to North American *Argia* Larvae (After Westfall and May 1996)

1. Lateral gills with marginal fringe of stout setae for at least ¾ their length on both the ventral and dorsal margins (taxa not included here)
1′. Lateral gills with marginal fringe of stout setae extending at most about ⅔ the length of the ventral margin only, much less on dorsal margin, sometimes nearly lacking 15
15(1′). Lateral gills with a fringe of stout setae extending along at least the basal ⅓ of the ventral margin 16
15′. Lateral gills with ventral setae absent or restricted to the basal ¼ of the ventral margin (taxa not included here)
16(15). Usually with 2 palpal setae; lateral gills either primarily dark or pale with a dark medial band and stout setae along basal ½ of dorsal edge of gill 17
16′. Usually with 3 or 4 palpal setae; lateral gills either primarily pale with dark mottling or pale with brown speckles, but not as above 20
17(16). Lateral gills more than 2.25× as long as wide; spiniform setae on at most basal 0.2 of dorsal margin; gill surface primarily dark with restricted light areas 18
17′. Length of lateral gills subequal to 2× their width; spiniform setae on basal ½ of dorsal margin; gill usually mostly pale with dark medial transverse band . . *munda*
18(17). Lateral gills almost uniformly dark; dorsum of abdomen either unmarked or with continuous broad pale dorsal stripe . . . 19
18′. Lateral gills primarily dark, but with pale basal area, central pale spot, and sometimes irregular pale areas as in Fig. 3b; dorsum of abdominal segments 9 and 10 with pale dorsal stripe, other segments variously patterned but without continuous dorsal stripe (Fig. 6) . . . . . *pima*
19(18). Ligula barely prominent, distinctly less convex than in *A. pima* (Fig. 2b); abdomen with broad, continuous pale middorsal stripe . . . . . *lacrimans*
19′. Ligula moderately prominent, at least as convex as in *A. pima* (Fig. 2b); dorsum of abdomen largely pale and without dorsal stripe . . . . . *tonto*
20(16′). Lateral gills 2.5–3× as long as wide, primarily pale but with extensive dark mottled areas or dark transverse bands; femora distinctly banded with bands narrower than spaces between them 21
20′. Lateral gills 2× as long as wide or less, surfaces pale with brown speckles; femora not distinctly banded or bands wider than intervening spaces . . . . . *alberta*
21(20). Abdomen with distinct, continuous, pale middorsal stripe 22
21′. Abdomen without a distinct pale middorsal stripe for its entire length; pale stripe usually present on segments 8–10

but does not extend through anterior segments (Fig. 1) . . . . . *sabino*

22(21). Lateral gill widest at or just beyond ½ its length, diffusely mottled (sometimes with faint transverse bands) . . . . . *anceps*

22'. Lateral gill widest at about ¾ its length, with 2 or 3 well-marked transverse bands . . . . . *tarascana*

Discussion

Argia sabino is very similar in adult morphology to *A. tarascana* Calvert, its sister species (Garrison 1994). The larvae of *A. tarascana* (Westfall 1990, Novelo-Guiterrez 1992) are similar to those of *A. sabino* as well, but in addition to the difference in abdominal color pattern described above, there also is a structural difference in female gonapophyses (especially as seen in lateral view). A parallel situation exists for *A. pima*; its sister species is *Argia lacrimans* Hagen (Garrison 1994). The larvae of these species are fairly distinct; beyond the characters used in our key, differences in the abdominal color pattern and the shape and setation of the male gonapophyses also distinguish the two species (compare with figures for *A. lacrimans* in Novelo-Guiterrez 1992).

Separating larvae of *A. sabino* and *A. pima* is an important objective for ecological and conservation studies in Sabino Canyon. No characters have been found to separate early-instar larvae of the two species, but for mature larvae this determination is not difficult provided well-formed lamellae are present. Lamellae are frequently absent or in early stages of regeneration in late-instar larvae. In this case, female larvae can be separated by a character of the gonapophyses: the inner pair of gonapophyses extends to the tips of the outer pair or beyond in *A. pima* (Figs. 5c, d), whereas the inner pair is recessed in *A. sabino* (Figs. 5a, b). Separation of males without lamellae is more difficult. In *A. pima,* the distance between the pharate cerci usually exceeds their width; in *A. sabino,* this gap is usually subequal to or less than the width of the cercus. Second, the stout setae on the gonapophyses of *A. sabino* are relatively few (fewer than 12 principal setae) and small. Stout setae are more numerous (more than 12 principal setae) and larger on the gonapophyses of *A. pima.*

Acknowledgments

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *NEASPILOTA WILSONI* BLANC AND FOOTE (DIPTERA: TEPHRITIDAE) ON *HAZARDIA SQUARROSA* (HOOKER AND ARNOTT) E. GREENE (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Neaspilota wilsoni* Blanc and Foote is a univoltine, monophagous fruit fly (Diptera: Tephritidae) developing in the flower heads of *Hazardia squarrosa* (Hooker and Arnott) E. Greene in southern California. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The egg pedicel is conical and completely circumscribed by many, shallow aeopyles of various sizes. The mouth hooks of all three instars are bidentate. The intersegmental areas of the first instar bear minute acanthae of a heretofore unreported form, i.e., cylindrical and apically bearing one to five prongs. Also newly reported, the caudal segment of the first instar bears stelex sensilla, each basally ringed with one to three, upright, pointed acanthae. The integumental petal is laterally fused with the stomal sense organ in the first instar, but separate in the second instar. The larvae feed mainly on the ovules and soft achenes as first and second instars; however, as third instars, they usually extend their feeding into the receptacle and additionally feed on sap that collects in the shallow scars. The nonfeeding prepuparium overwinters in a protective cell that occupies much of the excavated flower head and is formed of floret, pappus, and achene fragments impregnated with excess sap and liquid feces that harden when dry. A few prepuparia pupariate and emerge as adults in the fall and overwinter, but most pupariate in late winter to early spring, and emerge as adults that aggregate in summer on preblossom host plants to mate and subsequently oviposit. A single male specimen of *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae) was reared from a puparium of *N. wilsoni* as a solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Neaspilota, Hazardia, Haplopappus*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, seed predation, parasitoids

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae (Goeden 1989), and stimulated several life-history studies, including one on *N. viridescens* Quisenberry (Goeden and Headrick 1992). This paper describes the immature stages and life history of a second species from California, *Neaspilota wilsoni* Blanc and Foote.

MATERIALS AND METHODS

The present study was based in large part on dissections of subsamples of flower

heads of *Hazardia squarrosa* (Hooker and Arnott) E. Greene [= *Haplopappus squarrosus* (Hickman 1993)] collected during 1989–1995 from three locations in San Diego Co. in the manner described by Goeden (1985, 1989, 1992): W of Dogpatch along State Hwy. 94 at 760-m elevation; Los Terrenitos N of Interstate Hwy. 8 and junction with State Hwy. 79 at 1,000 m; Kitchen Creek Road above Cibbetts Flat Campground at ca. 1,300 m, Cleveland Nat. Forest. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Six eggs, four first-, three second-, and four third-instar larvae, and three puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stopped with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Single pairs of virgin males and females obtained from emergence cages also were held in each of six, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1998a, b), Goeden and Headrick (1992), Goeden and Teerink (1997; 1998; 1999a, b, c), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *N. wilsoni* adults and immature stages and its parasitoid reside in the research collections of RDG.

Results and Discussion

Taxonomy

Adult.—*Neaspilota wilsoni* was described by Blanc and Foote (1961) from a male from Jacolitas Canyon, Fresno Co., California. Foote and Blanc (1963) and Foote et al. (1993) pictured the unpatterned wing, as did Freidberg and Mathis (1986) along with drawings of the lateral aspect of the head, male right foretarsus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The egg, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Twenty-three ova dissected from five, 40+ days-old *N. wilsoni* plus 10 eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.93 ± 0.009 (range, 0.82–1.00) mm long, 0.24 ± 0.006 (range, 0.18–0.25) mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel conical, 0.02 mm long, completely circumscribed by different sized, mostly circular, shallow aeropyles, through which the spongy inner layers of the chorion are readily visible (Fig. 1B).

The egg of *N. wilsoni* is similar in shape,

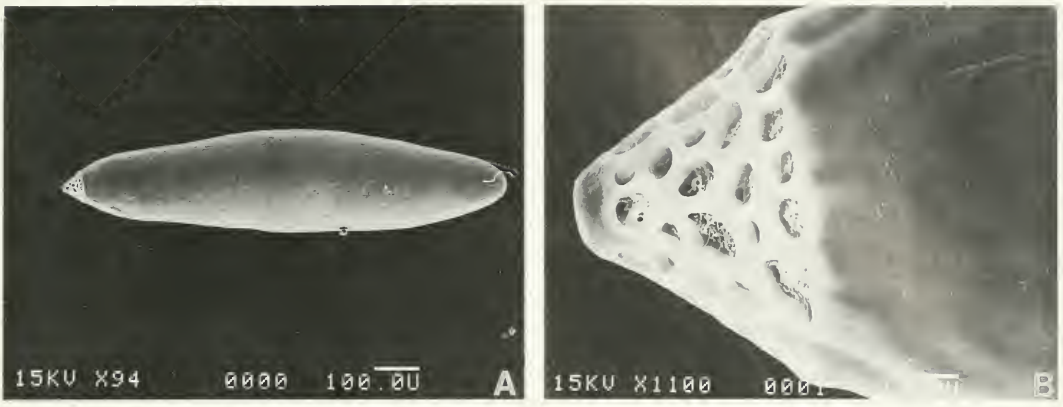

Fig. 1. Egg of *Neaspilota wilsoni:* (A) habitus, anterior end to left; (B) pedicel, aeropyles.

but about 40% longer and 30% wider than that of *N. viridescens* (Goeden and Headrick 1992); moreover, the latter species has fewer aeropyles that are irregularly and less densely spaced around its otherwise similarly-shaped and -sized pedicel. The eggs of 12 species of *Trupanea* from California studied to date, including *T. femoralis* (Thomson), *T. nigricornis* (Coquillett), and *T. wheeleri* Curran that occur in symphagy with *N. wilsoni* in heads of *H. squarrosa* (Goeden 1985, 1992, 1997), have pedicels circumscribed by only one or two rows of aeropyles (Goeden and Teerink 1999b and references therein).

First instar: White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (not shown); minute acanthae, pointed to cylindrical and apically one- to five-pronged, circumscribe intersegmental lines (Fig. 2A-1, C-1)$_S$ gnathocephalon smooth, lacking rugose pads, but with pair of prominent integumental petals dorsal to mouthhooks (Fig. 2A-2, B-1); dorsal sensory organ a dome-shaped papilla (Fig. 2A-8, B-2); anterior sensory lobe (Fig. 2A-4, B) bears the terminal sensory organ (Fig. 2A-5, B-3), pit sensory organ (Fig. 2B-4), lateral sensory organ (Fig. 2B-5), and supralateral sensory organ (Fig. 2B-6); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 2A-6, B-7), integumental petal fused laterally with stomal sense organ (Fig. 2A-6, B-7); mouthhook bidentate (Fig. 2A-7); median oral lobe laterally flattened, apically pointed (Fig. 2A-8); pit sensillum laterad of dorsal sensory organ (Fig. 2B-8); four verruciform sensilla circumscribe gnathocephalon medially (Fig. 2A-9); metathoracic lateral spiracular complex with a spiracle (Fig 2C-2) and four, vertically aligned, verruciform sensilla posteriorad (Fig. 2C-3); caudal segment with two stelex sensilla, dorsolaterad and ventrolaterad of posterior spiracular plates, each stelex sensillum basally ringed with one to three, upright, pointed acanthae (Fig. 2D-1); posterior spiracular plate bears two ovoid rimae, ca. 0.006 mm in length (Fig. 2D-2), and four interspiracular processes, each with five to nine branches, longest measuring ca. 0.01 mm (Fig. 2D-3); intermediate sensory complex with one stelex sensillum (Fig. 2D-4).

The first instar is similar in general habitus to that of *N. viridescens* (Goeden and Headrick 1992). However, unlike *N. viridescens*, the dorsal sensory organ of the first instar of *N. wilsoni* is well defined (Fig. 2A-3, B-2), as is the anterior sensory lobe and integumental petal. The reported poor definition of *N. viridescens* may have reflected specimen condition, as the same dissection and preparation procedures as well as scanning electron microscope were used with both species (but see descriptions of later instars below). Also, the pit sensory organ, not visible with *N. viridescens* (Goe-

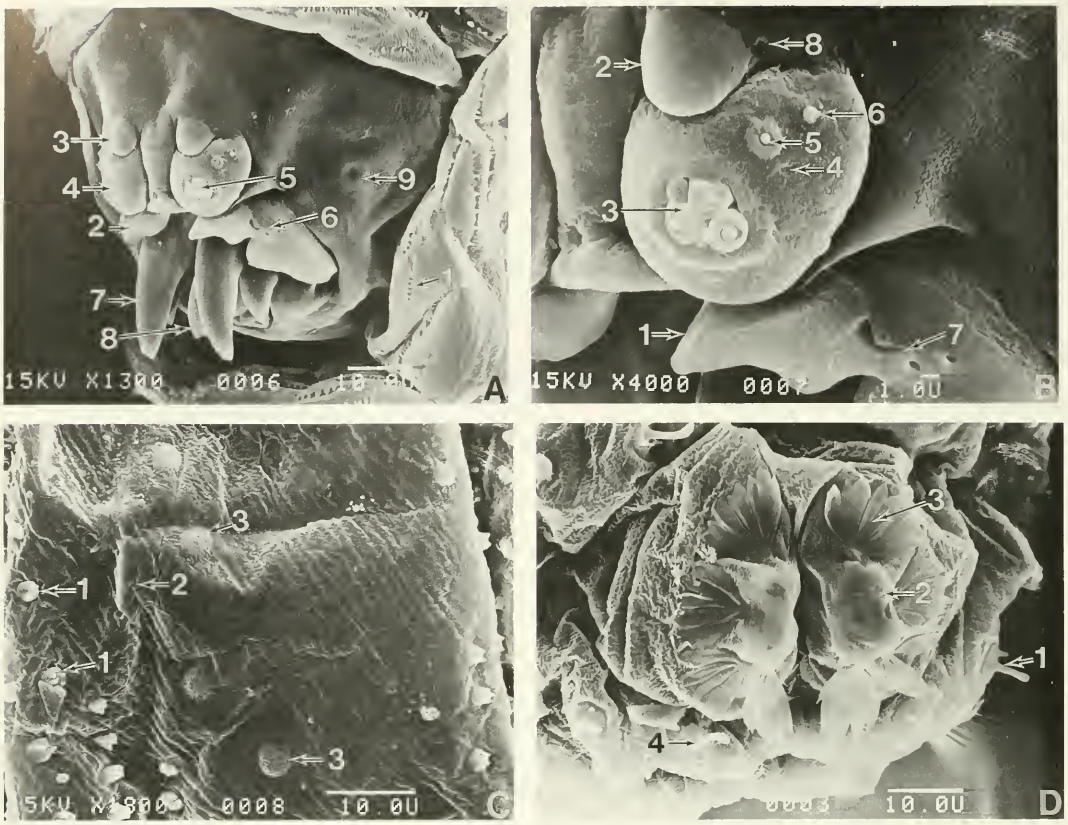

Fig. 2. First instar of *N. wilsoni:* (A) gnathocephalon, gnathocephalon, anterolateral view, 1- minute acanthae, 2- integumental petal, 3- dorsal sensory organ, 4- anterior sensory lobe, 5- terminal sensory organ, 6- stomal sense organ, 7- mouthhook, 8- median oral lobe, 9- campaniform sensillum; (B) anterior sensory lobe, 1- integumental petal, 2- dorsal sensory organ, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ, 8- pit sensillum; (C) metathoracic spiracular complex, 1- minute acanthae, 2- spiracle, 3- campaniform sensillum; (D) caudal segment, 1- stelex sensilla, with basal acantha, 2- rima, 3- intrespiracular process, 4- intermediate sensory complex, stelex sensillum.

den and Headrick 1992), is clearly seen in *N. wilsoni* (Fig. 2B-4). A fused integmental petal and stomal sense organ also was reported in first instar *Trupanea vicina* (Goeden and Teerink 1999b).

The cylindrical, apically pronged acanthae that circumscribe the intersegmental lines are the first of this type reported from tephritid larvae, as are the lateral stelex sensilla on the caudal segment that are basally ringed with upright, pointed acanthae. The 10 stelex sensilla reported to surround the posterior spiracular plate of the first instar of *N. viridescens* (Goeden and Headrick 1992) are suspect in number. These sensilla apparently are reduced to four in *N. wilsoni* (Fig. 2D-1, D-4), two sensilla less than the six reported for California *Trupanea* (Goeden and Teerink 1999b and references therein). As another difference, the interspiracular processes of *N. viridescens* have up to four branches (Goeden and Headrick 1992); whereas, *N. wilsoni* possesses up to nine branches (Fig. 2D-3). Needless-to-say, comparative studies of first instars of additional *Neaspilota* spp. are needed to better clarify these contradictory, apparent or real distinctions, which hopefully will be forthcoming in our next several papers.

Second instar: White, elongate-cylindri-

cal, tapering anteriorly, rounded posteriorly (not shown), minute acanthae circumscribe intersegmental lines (Fig. 3A-1, D-1)$_S$ gnathocephalon conical (Fig. 3A); dorsal sensory organ a dome-shaped papilla (Fig. 3A-2, B-1); anterior sensory lobe (Fig. 3A-3, B) bears the terminal sensory organ (Fig. 3A-4, B-2), lateral sensory organ (Fig. 3B-3), supralateral sensory organ (Fig. 3B-4), and pit sensory organ (Fig. 3B-5); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 3B-6, C-1); mouthhook bidentate (Fig. 3A-5, C-2); median oral lobe laterally flattened (Fig. 3C-3); two pit sensilla laterad of dorsal sensory organ (Fig. 2B-7); labial lobe with two pore sensilla (Fig. 3C-4); single row of integumental petals dorsal to mouthhook (Fig. 3A-6, B-8, C-5); most oral ridges lateral to mouthhooks dentate along posterior margins (Fig. 3A-7, C-6); pit sensilla circumscribe gnathocephalon medially (Fig. 2A-8); anterior thoracic spiracle with three to four oblong papillae; lateral spiracular complex of mesothorax with a spiracle (Fig. 3D-2) and three verruciform sensilla in vertical row (Fig. 3D-3); caudal segment with at least two stelex sensilla (not shown), dorsolaterad and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.014 mm in length (Fig. 3E-1), and four interspiracular processes, each with two to six branches, longest measuring 0.011 mm (Fig. 3E-2); intermediate sensory complex with a stelex sensillum (Fig. 3F-1) and a medusoid sensillum (Fig. 3F-2).

Few differences were noted between the first and second instars, besides the acquisition of prothoracic spiracles and another rima on the posterior spiracular plate normal to all tephritid larvae (Headrick and Goeden 1998). The dorsal sensory organ is less well defined in the second instar (Fig. 3A-2, B-1) than in the first instar (Fig. 2A-3, B-2). However, the habitus of the second instar of *N. viridescens* was described as barrel-shaped (Goeden and Headrick 1992); whereas, that of *N. wilsoni*, is elongate cylindrical, like the first instars of both species. Another distinction between the first and second instar of *N. wilsoni* is the presence of seven oral ridges with dentate margins in the latter instar, also pictured and equal to, but unquantified until now (unpublished data), for the second instar of *N. viridescens* (Goeden and Headrick 1992). The stomal sense organs of both species bear three sensory structures, described as conical in *N. viridescens* (Goeden and Headrick 1992), but which appear papilliform in *N. wilsoni* (Fig. 3B-6, C-1). The mouth hooks of the second instar of *N. viridescens* are tridentate (Goeden and Headrick 1992); whereas, those of *N. wilsoni* are bidentate (Fig. 3A-5, C-2). Similar, apparent interspecific differences in dentation were noted among mouth hooks of second instar *Trupanea* spp. (Goeden and Teerink 1999b and references therein). Finally, the stelex sensilla on the caudal segment of the second instar of *N. wilsoni* are not basally ringed by pointed acanthae (Fig. 3F-1), as in the first instar (Fig. 2D-1); the interspiracular processes each bear two to six (Fig. 3E-2), not five to nine branches (Fig. 2D-3), respectively; and the intermediate sensory complex consists of a medusoid and a stelex sensillum (Fig. 3F-1, 2), not just a single stelex sensillum (Fig. 2D-4). In contrast, the interspiracular processes of the second instar of *N. viridescens* were noted to be two-branched at most (Goeden and Headrick 1992). Again, comparative studies of second instars of additional species of *Neaspilota* are needed in order to help distinguish real from apparent, intra- and interspecific differences.

Third instar: Mostly white, with last two or three segments darkened, elongate-cylindrical, tapering anteriorly, posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60°, minute acanthae circumscribe all intersegmental areas and all abdominal segments except pleura (Fig. 4A, F)$_S$ gnathocephalon conical (Fig. 4B); apparently six oral ridges laterad of mouth lumen, all with serrated margins (Fig. 4B-

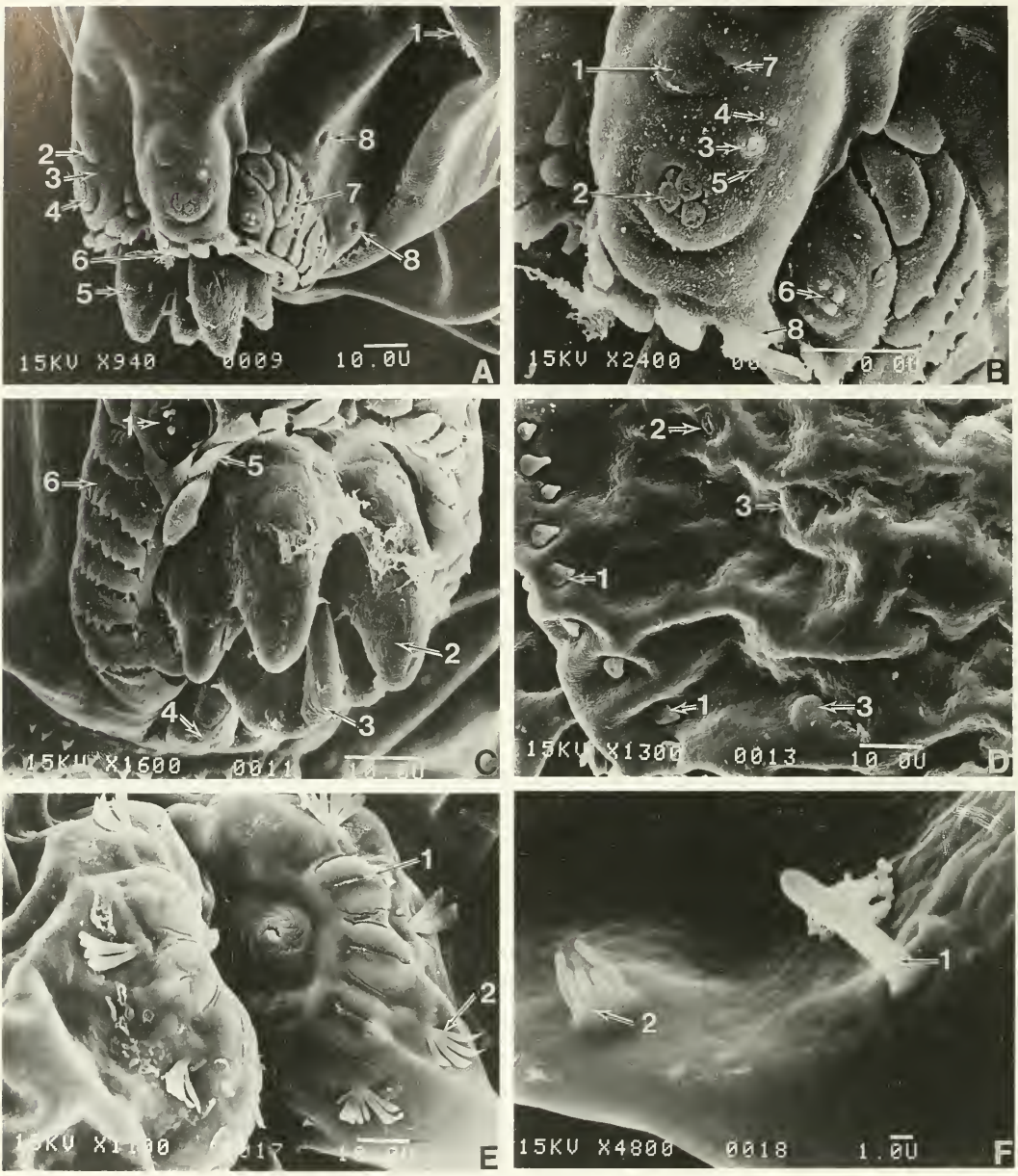

Fig. 3. Second instar of *Neaspilota wilsoni:* (A) gnathocephalon and prothorax, anterolateral view, 1- minute acanthae, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- terminal sensory organ, 5- mouth hook, 6- integumental petal, 7- oral ridge, 8- pit sensilla, (B) anterior sensory lobe, 1- dorsal sensory organ, 2- terminal sense organ, 3- lateral sensory organ, 4- supralateral sensory organ, 5- pit sensory organ, 6- stomal sensory organ, 7- pit sensillum, 8- integumental petal, (C) gnathocephalon, ventrolateral view, 1- stomal sense organ, 2- mouthhook, 3- median oral lobe, 4- labial lobe, 5- integumental petal, 6- oral ridge; (D) metathoracic spiracular complex, 1- minute acanthae, 2- spiracle, 3- campaniform sensilla; (E) caudal segment, 1- rima, 2- interspiracular process; (F) intermediate sensory complex, 1- stelex sensillum, 2- medusoid sensillum.

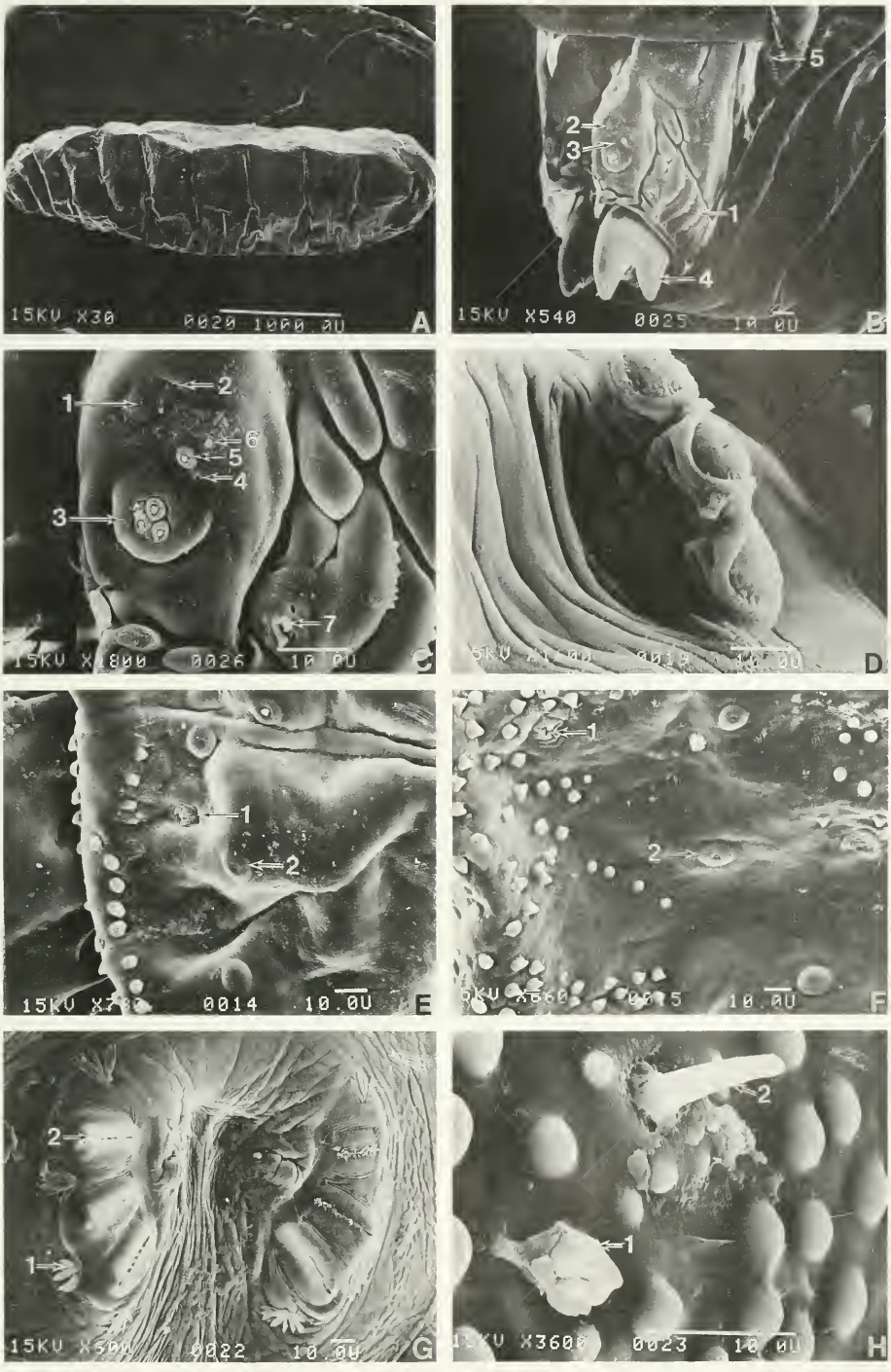

Fig. 4. Third instar of *Neaspilota wilsoni:* (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1- oral ridge, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- mouthhook, 5- minute acanthae; (C) anterior sensory lobe, 1- dorsal sensory organ, 2- pit sensillum, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ; (D) anterior thoracic spiracle; (E) metathoracic spiracular complex, 1- spiracle, 2- campaniform sensillum; (F) first abdominal spiracular complex, 1- spiracle, 2- campaniform sensillum; (G) caudal segment, 1- interspiracular process, 2- rima; (H) intermediate sensory complex, 1- medusoid sensillum, 2- stelex sensillum.

1); dorsal sensory organ a dome-shaped papilla (Fig. 4B-2, C-1), pit sensillum laterad of dorsal sensory organ (Fig. 4C-2); anterior sensory lobe (Fig. 4B-3, C) bears the terminal sensory organ (Fig. 4C-3), pit sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), and supralateral sensory organ (Fig. 4C-6); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 4C-7); mouth hook bidentate (Fig. 4B-4); median oral lobe not clearly visible; prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-5); anterior thoracic spiracle bears three oblong papillae (Fig. 4D); metathoracic lateral spiracular complex with a spiracle (Fig. 4E-1) and four verruciform sensilla (Fig. 4E-2); abdominal lateral spiracular complex with a spiracle (Fig. 4F-1), three verruciform sensilla (Fig. 4F-2); caudal segment circumscribed by minute acanthae; stelex sensilla, dorsolaterad, laterad and ventrolaterad of posterior spiracular plate; posterior spiracular plate bears three ovoid rimae, ca. 0.013 mm in length (Fig. 4G-2), and four interspiracular processes (Fig. 4G-1), each with three to four branches each with one to three, apical teeth, longest branch measuring 0.012 mm; intermediate sensory complex with a medusoid (Fig. 4H-1) and a stelex sensillum (Fig. 4H-2).

The habitus of the third instar of *N. wilsoni* generally is like that reported for *N. viridescens* by Goeden and Headrick (1992), except that minute acanthae circumscribe all intersegmental areas and all abdominal segments except the pleura in the former species; whereas, in the latter species the intersegmental areas are free of acanthae. Like the second instar of *N. wilsoni*, the dorsal sensory organ is less well defined in the third instar (Fig. 4B-2, C-1) than in the first instar (Fig. 2A-3, B-2). The dorsal sensory organ in the third instar *N. viridescens* also is not well defined, but this is not a generic character (unpublished data), as proposed by Goeden and Headrick (1992). The stomal sense organs of the third instars of both species bear sensory structures, described as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992), but which appear papilliform and pit-type in *N. wilsoni* (Fig. 4C-7). Unlike the second instar of *N. wilsoni*, the third instar apparently has six oral ridges, all with dentate margins, the same as partially pictured, but unquantified, and also now reported for the third instar of *N. viridescens* (Goeden and Headrick 1992 and unpublished data). This may represent a loss from the second instar of one oral ridge in the third instar of both species; however, distinguishing and accurately counting these structures is rendered problematic by degree and angle of exposure of the gnathocephalon as well as by a current lack of a precise definition for and defined morphological limits to these structures (Tesky 1981). The third instars of *Trupanea imperfecta, T. jonesi, T. nigricornis, T. pseudovicina, T. signata*, and *T. wheeleri* also bear serrated oral ridges (Goeden and Teerink 1997; 1998, 1999b; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1998). Also, like the second instar, the mouthhooks of third instar *N. wilsoni* are bidentate (Fig. 4B-4); whereas, those of *N. viridescens* are tridentate (Goeden and Headrick 1992). Such interspecific differences in dentation are supported by our findings that the mouth hooks of third instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 1999b and citations therein). The abdominal lateral spiracular complex is like that pictured and described for third instar *Stenopa affinis* Quisenberry (Goeden and Headrick 1990).

Puparium: Mostly white to yellow, with posterior two-three segments grayish to blackened posteriorly, broadly ellipsoidal and smoothly rounded at both ends, minute acanthae circumscribe intersegmental lines; anterior end bears the invagination scar (Fig. 5A-1) and anterior thoracic spiracles (Fig. 5A-2); caudal segment circumscribed by minute acanthae (Fig. 5B-1), two stelex

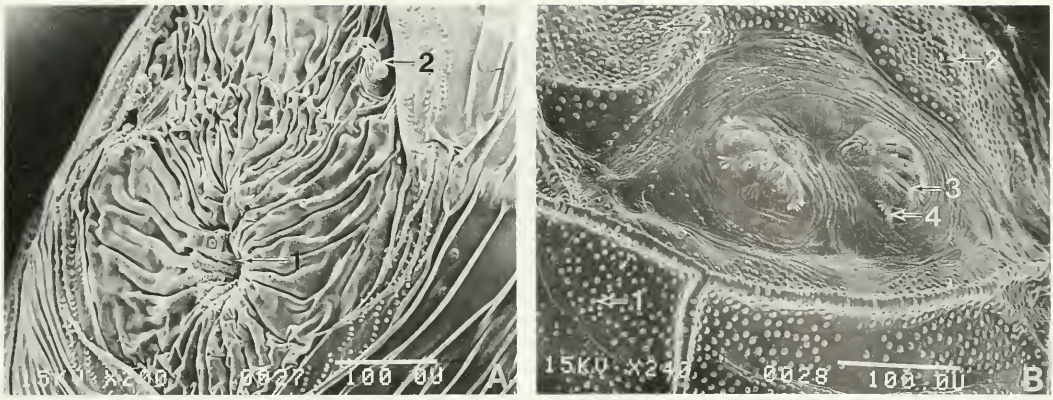

Fig. 5. Puparium of *Neaspilota wilsoni:* (A) anterior end, 1- invagination scar, 2- anterior thoracic spiracle, (B) caudal segment, 1- minute acanthae, 2- stelex sensillum, 3- rima, 4- interspiracular process.

sensilla, dorsad and ventrad of posterior spiracular plates (Fig. 5B-2); posterior spiracular plate bears three broadly elliptical rimae (Fig. 5B-3), and four interspiracular processes, each with 3 to 4 branches (Fig. 5B-4); intermediate sensory complex with a medusoid sensillum and a stelex sensillum. Six puparia averaged 2.75 ± 0.16 (range, 1.99-3.11) mm in length; 1.24 ± 0.03 (range, 1.12-1.32) mm in width.

Distribution and Hosts

The distribution of *N. wilsoni* as mapped by Foote et al. (1993) restricted this tephritid to California in the United States north of Mexico. The distribution of this true monophage probably also extends southward into northern Baja California like that of its only known host plant, *H. squarrosa* (Freidberg and Mathis 1986, Goeden 1989, Foote et al. 1993), commonly known as "saw-toothed goldenbush" (Hickman 1993), which belongs to the subtribe Solidagininae in the tribe Astereae (Bremer 1994). We here reiterate our belief (Goeden 1989) reported by Foote et al. (1993) that the unconfirmed record for *Coreopsis calliopsidea* Gray in Freidberg and Mathis (1986), which they suspected was a host, probably is not valid, owing to its distant relationship to *Hazardia*; it belongs to the tribe Heliantheae, subtribe Coreopsidinae (Bremer 1994). Furthermore, neither *N. wilsoni*, nor any other species of *Neaspilota*, has ever been reared from the genus *Coreopsis* in California (Goeden 1989), even during intensive and extensive field study of two principal associates of *Coreopsis* spp., *Dioxyna picciola* (Bigot) (Headrick et al. 1996) and *Trupanea jonesi* Curran (Goeden et al. 1998a).

Biology

Egg.—In 17 closed, preblossom, apical or penultimate, immature flower heads of *H. squarrosa*, 19 eggs were inserted between or through the phyllaries, usually into or between the inner phyllaries, and perpendicular or at a slight angle (ca. 15°) to the receptacle (Fig. 6A). All eggs were oviposited pedicel-last. Only one flower head contained a floret damaged by oviposition. The diameters of the receptacles of 17 flower heads containing eggs averaged 1.8 ± 0.2 (range, 0.85–3.75) mm, and these heads contained an average of 1.1 ± 0.1 (range, 1–2) eggs.

Larva.—Upon eclosion, first instars tunneled through an inner phyllary into the apical end of an ovule. An average of 1.3 ± 0.2 (range, 1–3) first instars was found feeding within each of 10, closed, preblossom flower heads, the receptacles of which averaged 1.6 ± 0.2 (range, 1.1–2.0) mm in diameter. These infested heads contained an average of 17 ± 1 (range, 15–18) ovules,

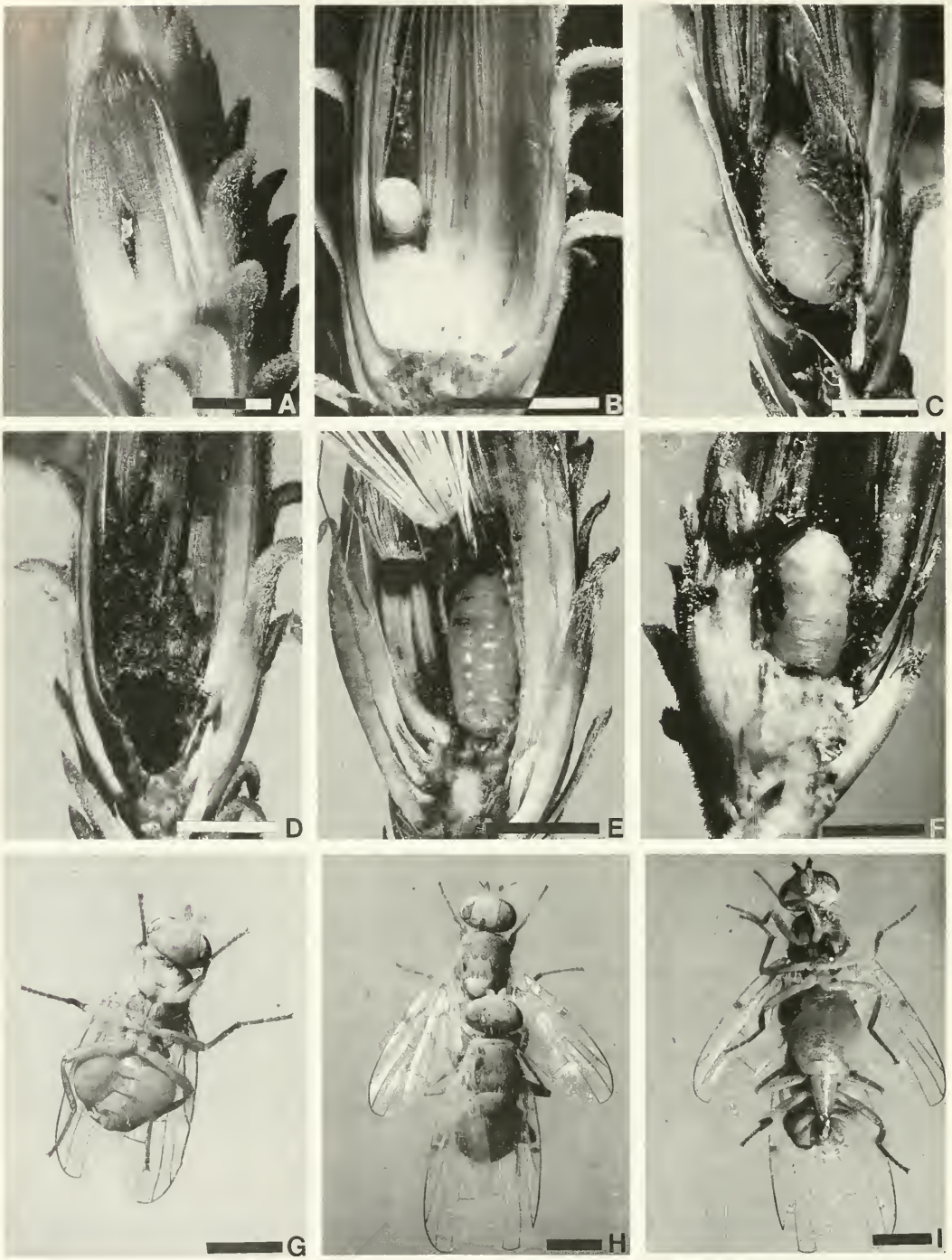

Fig. 6. Life stages of *Neaspilota wilsoni:* (A) egg laid in immature flower head of *Hazardia squarrosa*, (B) second instar feeding on soft achene in open flower head, (C) third instar feeding among soft achenes in center of open flower head, (D) partially opened cell in flower head, (E) prepuparium in flower head, (F) puparium in flower head, (G) male with expanded abdominal pleura, ventral view, (H) mating pair, dorsal view; (I) mating pair, ventral view. Lines = 1 mm.

of which only one or two, or about 8% (range, 6–13%), were damaged. First instars continued to feed on the ovules, most with their mouthparts directed towards the receptacles. No receptacles within these 10 infested flower heads were abraded or pitted by first instar feeding.

Second instars fed mainly in ovules of preblossom flower heads or in soft achenes of open heads (Fig. 6B). About half fed with their bodies perpendicular to and their mouthparts directed towards the receptacles; the others fed horizontal to the receptacles within adjacent ovules/soft achenes, but still well above the receptacles (Fig. 6B). Receptacles of eight flower heads containing second instars were undamaged and averaged 1.7 ± 0.1 (range, 1.4–2.0) mm in diameter. These flower heads each contained a single second instar that had destroyed an average of 4.5 ± 1.2 (range, 1–12) ovules/soft achenes, or about 26% (range, 5–46%) of an average total of 15 ± 1.6 (range, 11–22) ovules/soft achenes.

Third instars fed mainly on ovules or soft achenes in the centers of closed or postblossom flower heads, respectively (Fig. 6C). In 24 flower heads averaging 1.8 ± 0.6 (range, 1.4–2.3) mm in diameter and containing an average of 1.0 ± 0.04 (range, 1–2) third instars, from eight to all of the ovules/soft achenes therein were damaged, or about 60 to 100% of an average total of 14 soft achenes per head contained in a separate subsample of 47 uninfested, mature flower heads. Third instars in flower heads fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 6C). Two-thirds of the third instars in the 24 infested heads scored or pitted the receptacles, or used the basal stumps of achenes as conduits, and thus supplemented their diet with sap. Goeden and Headrick (1992) described and discussed this similar type of feeding by *N. viridescens*. And, as they also reported for *N. viridescens*, the third instar became surrounded for about 90% its length by a cell, which occupied most of the interior of the flower head and consisted of ovule-, achene-, pappus-, and floral tube-fragments cemented together by liquid feces and sap that hardened when dry (Fig. 6D). These protective cells externally incorporated the outer walls of achenes and the few uneaten achenes, were blackened and smooth inside, and averaged 2.4 ± 1.4 (range, 1.0–3.8) mm long by 1.8 ± 0.4 (range, 0.8–2.6) mm wide and about 0.2 mm in wall thickness (Fig. 6D). Upon completing their feeding and cell construction, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed prepuparia (Headrick and Goeden 1998). Most individuals overwintered in diapause as prepuparia (Fig. 6E) (Goeden and Headrick 1992, Headrick and Goeden 1998), but <10% pupariated (Fig. 6F).

Pupa.—Puparia (Fig. 6F) formed in flower heads in the fall produced adults that emerged by pushing aside the loose plug of excised pappus bristles and other debris at the cell apex. A portion of those few adults that emerged earliest possibly matured, mated, and produced a small partial second generation on late-formed flowerheads, while the few other adults that emerged later probably remained sexually immature and overwintered, like some other monophagous, aggregative tephritids, to reproduce when their hosts again flowered (Headrick and Goeden 1994, 1998).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 14 unmated males averaged 66 ± 13 (range, 11–147) days, and 13 virgin females averaged 92 ± 15 (range, 19–171) days. Such lengthy longevities are commensurate with the aggregative type of life cycle described below for this tephritid, and compare favorably with average adult longevities of 87 and 86 days, respectively, reported for male and female *N. viridescens* (Goeden and Headrick 1992).

The premating and mating behaviors of *N. wilsoni* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other noncongener-

ic, nonfrugivorous, tephritid species (Headrick and Goeden 1994), including *N. viridescens* (Goeden and Headrick 1992). Premating behaviors observed with *N. wilsoni* were abdominal pleural distension (Fig. 6G), side-stepping, and swaying by males (Headrick and Goeden 1994), and wing hamation by both sexes (Headrick and Goeden 1994). However, no trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). Four matings were observed during the early afternoon with different pairs of flies of 255-, 175-, 145-, 140-min duration and one late-morning mating that lasted 235 min; similarly long mating durations were reported with *N. viridescens* by Goeden and Headrick (1992). Disengagement, rarely observed in *Neaspilota* spp. (Headrick and Goeden 1994), was seen once and involved a male turning 180° as he rapidly dismounted and walked away from the female while pulling free his genitalia, as reported with other genera (Headrick and Goeden 1994, Goeden and Teerink 1999b). No post-copulatory behavior was observed other than individual groomings by both flies, and the male storing his genitalia.

Seasonal history.—The life cycle of *N. wilsoni* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the long-lived prepuparia are the principal overwintering stage contained in cells in dead flower heads that remain attached to plants. Come late winter to early spring (February–April), following pupation, the adults emerge and join the few surviving overwintered adults to aggregate in summer (June–August) on long-flowering *H. squarrosa* for mating and oviposition to complete the life cycle. As noted above, a small partial second generation may be produced, although *N. wilsoni* principally is a univoltine species.

Natural enemies.—A single male specimen of *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae) was reared from a puparium of *N. wilsoni* as a solitary, larval-pupal endoparasitoid.

Acknowledgments

We thank Andrew C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, for identifications of plants mentioned in this paper. The parasitoid was identified by Michael Gates, Department of Entomology, University of California, Riverside, and Harry E. Andersen, Huntington Beach, California. We also are grateful to Kristine Gilbert and Jeff Teerink for their technical assistance and to Louie Blanc and Jeff Teerink for their helpful comments on earlier drafts of this paper.

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NOTE

New Record of a Parasitoid (Hymenoptera: Eulophidae) of the European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae)

The European corn borer (ECB), a pest species introduced to the U.S. in the early 1900s, is one of the most serious pests of corn (*Zea mays* L.) in the United States. European corn borer infests crops over a wide geographic area east of the Rocky Mountains south through Texas, east to the Atlantic coast, and northward into southern Canada (European corn borer home page-http://www.ent.iastate.edu/pest/cornborer). *Ostrinia nubilalis* (Hübner), while usually considered a corn pest, feeds on over 200 plants, including potato, pepper, celery, and tomato (European corn borer-http://ipmwww.ncsu.edu/AG295/html/european_corn_borer.htm) and may cause significant damage to those crops in some cases (European corn borer damage to peppers-http://www.ianr.unl.edu/pubs/nebfacts).

Ostrinia nubilalis is parasitized by several different parasitic Hymenoptera, including members of the Braconidae, Ichneumonidae, Pteromalidae, Chalcididae, Elasmidae, Trichogrammatidae, and Eulophidae (Noyes, J. S. 1998. CD-ROM, Biodiversity Center of ETI, Amersterdam, Netherlands). Among the Eulophidae, parasitoids in the genera *Hemiptarsenus, Eulophus, Sympiesis,* and *Tetrastichomyia* have been recorded.

In August 1996, a series of parasites was reared from the larvae and pupae of ECB collected near Auburn, Illinois (Sangamon Co.), in the east-central part of the state. These specimens were submitted to the Systematic Entomology Laboratory, USDA, for determination in November of 1998 and identified as *Pediobius facialis* Giraud (Eulophidae). A search of the literature revealed that *P. facialis* has not been previously recorded from ECB.

Pediobius facialis is a known pupal parasitoid of a number of different Lepidoptera, including species of Noctuidae, Olethreutidae, Hesperiidae, Tortricidae, and Gelechiidae (Peck 1985. Canadian Entomologist 117:647–704). The distribution of *P. facialis* includes most of Europe and much of eastern North America. It was recorded in North America as *P. sexdentatus* (Girault) until 1985. It is believed to function as both a primary and secondary parasitoid and there are several host records of it being reared from ichneumonids and braconids. This species is usually gregarious and may have more than one generation per year.

A specimen of *P. facialis* reared from ECB has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

M. E. Schauff, *Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Washington, DC 20560-0168, U.S.A. (e-mail: mschauff@sel.barc.usda.gov)*

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Obituary

Alan Stone
1904–1999

Alan Stone, eminent dipterist, died on March 4, 1999 at the age of 95. He was a lifelong member and generous benefactor of the Entomological Society of Washington, and was one of its Honorary Members. He served the Society as Editor from 1944 to 1947, as President in 1951, and was a regular attendee at meetings and the annual banquet. He was a lifelong member also of the Entomological Society of America.

Alan was born in Brooklyn, New York, on January 23, 1904. He graduated from Cornell University in 1926 and earned his doctorate there in 1929 with a thesis on North American Tabanidae. On August 25, 1928, he and Louise Beaujon were married. He taught one year at Dartmouth University and then on October 21, 1931 began his forty-year long employment as a biting fly specialist with what is now the Systematic Entomology Laboratory of the U.S. Department of Agriculture at the Smithsonian Institution in Washington, DC. He served as the supervisor of the Diptera Unit from its establishment in the 1930s until his retirement on December 31, 1971.

He authored or coauthored about 100 papers, chiefly on mosquitoes, blackflies, and horseflies. His most important contribution was his work on mosquitoes, especially during World War II and the Korean War when there were exceptionally heavy demands on him for identification of specimens from all parts of the world, particularly the Pacific Islands and Southeast Asia. He identified 7,000 to 9,000 samples during each of the WW II years, much of it new to science, and instructed approximately 200 Army, Navy, and Public Health Service officers in mosquito identification. Kenneth L. Knight, assigned for a year and a half as a Navy officer during the Second World War to study Pacific mosquitoes with Alan, remembers how calm and unruffled he was through the constant intrusions by visiting Armed Forces personnel, all the while keeping abreast of his regular duties without technical help. These busy years were the foundation for the innovative *Synoptic Catalog of the Mosquitoes of the World* by Stone, K. L. Knight, and H. Starcke published in 1959, the first catalog of the entire

family to appear in 37 years during which time names of mosquitoes had tripled in number. That catalog lives on, subsumed and updated in 1977 by *A Catalog of the Mosquitoes of the World* authored by Knight and Stone.

One of Alan's great accomplishments followed from a special project he was assigned just before the War, to revise the tephritid genus *Anastrepha*, an economically important group then receiving a lot of attention in Central America. No one else was available in the Laboratory then to cover plant-feeding flies, normally outside his USDA assignment. He responded with a fine revision of the genus that appeared in 1942, in which were described 104 species, including 52 new to science. That publication was authoritative and timely, and is still used today by fruit fly specialists.

His epitaph should probably be *A Catalog of the Diptera of America North of Mexico* published in 1965. It was in fact a team effort of the Diptera Unit, but he headed the program, there was no doubt. His correspondence with collaborators for that volume was immense and the care for the punchcard system that was used was a painstaking operation. The catalog, used now by some entomologists not even born when Alan retired, was the catalyst for all the regional Diptera catalogs that have followed.

Alan was a conscientious, meticulous worker, a prompt and excellent correspondent, equally responsive to each of the separate tasks of his job: research, curation, and service. The Diptera families within his responsibility were the best curated and cataloged. Alan had a habit of abstracting current taxonomic literature onto index cards at home in the evenings. His first task upon coming to work in the morning was to file the cards, the occasional second was to write other taxonomists notifying them of homonyms they had created. One of Alan's daily customs was to post outside his office door a New Yorker cartoon, a new one on top of the previous ones throughout the week. On Monday he discarded them all and started a new series.

He was unpretentious, gentlemanly, cultivated, and well read, particularly on issues of the day and politics, and had a definite liberal inclination. He was good-humored and would chuckle over a good joke, but was generally laconic and had not much time for small talk. His phone conversations were polite but short and almost abrupt. He never took coffee breaks, had his lunch always in under 30 minutes in one of the government cafeterias nearby, and no one can remember him engaging in idle conversation.

He kept perhaps the neatest office at the Museum. On the day he retired, his desk was ready for a new occupant to sit down and begin work, completely clear except for a sheet of paper advising that the literature files and card files were in alphabetical order by family, genera, and species, and indicating where the various families that had been under his purview were located in the general collection. He had some manuscripts in press to proofread, but beyond that left no unfinished business. Alan chose not to continue taxonomic work after he retired, believing that no one was irreplaceable. He had many other interests, including philately until his extensive stamp collection as well as other prized possessions were stolen by a burglar, but retained a keen interest in entomology and entomologists. In 1980 his history of Nearctic dipterology prepared for the *Flies of the Nearctic Region* was published.

He and his wife Louise hosted many dipterist and other gatherings at their home. Louise was a gracious and socially astute hostess. They shared a large acquaintance among entomologists through her job in the office of the Entomological Society of America. Each year they bought four subscription theatre tickets and would serially treat dipterists and other friends and their wives to a play a year. Louise predeceased Alan in 1990. They are survived by their son Peter and daughter-in-law Marila of

Durham, North Carolina, and two granddaughters.

In recent years Alan wrote a limerick each day on his old manual typewriter. When friends visited or invited him somewhere, he would present them a sheet with 20 or so selections arranged in double column. The limericks allowed him to make pithy, humorous, or wry statements about important or homely events. He took some trouble over the titles so that they complemented the subjects perfectly. I have chosen four of them to publish here, the first of which gives me license to do so.

NO SALE

These limericks have no copyright
Use them and there will be no fight
  They are offered for free
  As they certainly should be.
It's not many that they would delight.

LITERARY

There once was a chap named Hawthorne
Who wrote what some thought was porn
  Hester Prynne was the harlot
  The letter was scarlet
Now young folks consider it corn.

TOO MANY

There was a man named Thomas Malthus
Who raised a very big fuss
  About not enough food
  For everyone's brood
But most thought he doesn't mean us.

NO ESCAPE

One who takes physical exercise
May somewhat postpone his demise
  But the grim reaper comes
  To good folks and bums
As everyone must realize.

Raymond J. Gagné, *Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0168, U.S.A. (e-mail: rgagne@sel.barc.usda.gov).*

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MEMBERSHIP LIST OF THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

The previous list was published in October 1996 with 401 members; the present list contains 429 members from every state in the union except Alaska, Maine, Massachusetts, and Nevada; Puerto Rico is included, as well. The largest representation is in Maryland (61), followed by the District of Columbia (44), California (30), Texas (16), and Ohio and Virginia (15 each). The figures from the Washington, D.C. area are slightly skewed since some members receive their Proceedings at office addresses. Five of the Canadian provinces are represented and 18 other countries, on five continents, are represented.

The format used in this list essentially follows that of the 1996 list. Names of Honorary Members are capitalized, those of Emeritus Members (25) are italicized, and Life Members are distinguished by an asterisk (28) following the date they joined the Society. Dates of election to Honorary or Emeritus status are entered in parentheses. In 1988 Dr. Louise M. Russell was elected Honorary Member. In 1993 Dr. Karl V. Krombein was elected Honorary Member. In 1998 Dr. Louise M. Russell was elected Honorary President and Ronald W. Hodges was elected Honorary Member. In 1999 Drs. Donald M. Anderson and William E. Bickley were elected Honarary Members.

I thank Dianne Mathis for her kind assistance in the preparation of this list. Any corrections to the list can be sent to the Corresponding Secretary at the address on the inside front cover of this issue. Corrections will be read at the next meeting of the Society, and will be published in the *Proceedings* by the Recording Secretary.

Holly B. Williams,
Corresponding Secretary

Abe, Masaki 1988 JAPAN
Abrahamson, W. G. 1997 Pennsylvania
Adams, J. R. 1963 Maryland
Adams, M. S. 1983 New York
Adamski, D. 1984 District of Columbia
Adler, P. H. 1986 South Carolina
Ahlstrom, K. R. 1992 North Carolina
Aitken, T. G. H. 1957 (1984) Connecticut
ANDERSON, D. M. 1954 (1999) Maryland
Anderson, L. D. 1944 (1989) California
Aarchangelesky, M. 1998 ARGENTINA
Armitage, B. J. 1983 Ohio
Arnaud, P. H., Jr. 1955 California

Baier, T. 1999 New Hampshire
Baker, G. T. 1987 Mississippi
Baker, R. H. 1992 Florida
Ball, G. E. 1948 Alberta
Balogh, G. J. 1994 Michigan
Barber, K. N. 1985 Ontario
Barnes, J. K. 1978 New York
Barrows, E. M. 1976 District of Columbia
Baumann, R. W. 1972 Utah
Baumgardner, D. E. 1992 Texas
Becker, V. O. 1987* BRAZIL
Bell, R. T. 1955 Vermont
Bellinger, R. G. 1972 South Carolina
Berry, R. L. 1972 Ohio
Bezark, L. G. 1974 California
Bicha, W. 1981 Tennessee
BICKLEY, W. E. 1949* (1999) Maryland
Bilby, P. J. 1993 New Jersey
Bilyj, B. 1998 Ontario
Blom, P. E. 1986 Idaho
Bohart, R. M. 1944 California
Borkent, A. 1988 British Columbia
Bowles, D. E. 1993 Texas
Brailovsky, H. 1996 MEXICO
Branham, M. A. 1998 Ohio
Bray, R. O. 1999 Maryland
Broda-Hydorn, S. 1991 Maryland
Brodel, C. F. 1991 Florida
Brou, V. A. 1985 Louisiana

Brown, B. V. 1993 California
Brown, H. P. 1977 Oklahoma
Brown, J. W. 1997 District of Columbia
Brown, R. L. 1979 Mississippi
Bruce, W. A. 1995 Maryland
Brushwein, J. R. 1987 Florida
Bueno-Soria, J. 1977 MEXICO
Burger, J. F. 1972 New Hampshire
Burke, H. R. 1981 Texas
Burns, J. M. 1975* District of Columbia
Burrows, W. L. 1983 West Virginia
Butler, L. 1966 West Virginia
Byers, G. W. 1984 Kansas

Calabrese, D. 1997 Maryland
Carlson, R. W. 1970* Maryland
Carroll, J. F. 1977 Maryland
Carroll, L. E. 1997 Maryland
Carvalho, C.J. Barros de 1995 BRAZIL
Cave, R. D. 1977 HONDURAS
Clark, W. E. 1975 Alabama
Clements, K. M. North Carolina
Cohen, E. A., Jr. 1999 Maryland
Connor, E. F. 1990 California
Contreras-Ramos, A. 1986 MEXICO
Cook, J. L. 1996 Texas
Cooper, K. W. 1955 California
Coovert, G. A. 1996 Ohio
Coulson, J. R. 1961 Maryland
Courneya, P. 1986 Florida
Courtney, G. W. 1985 Iowa
Covell, C. V., Jr. 1971 Kentucky
Cross, H. F. 1954 Georgia
Currie, D. C. 1999 Ontario

Darling, D. C. 1981 Ontario
Darsie, R. F. 1949 South Carolina
Davis, D. R. 1961 District of Columbia
Davis, L. R., Jr. 1992 Florida
Deeming, J. C. 1974* WALES
Deitz, L. L. 1982 North Carolina
Dennis, S. 1976 Colorado
Dewalt, R. E. 1992 Illinois
Deyrup, M. A. 1979 Florida
Disalvo, C. 1997 Virginia
Dodson, B. 1998 Virginia
Donnelly, T. W. 1962 New York
Dozier, H. L. 1952* South Carolina
Drummond, R. O. 1954 (1987) Texas
Duffield, R. M. 1996 District of Columbia
Durkin, P. 1999 District of Columbia

Easton, E. 1997 HONG KONG
Eckerlin, R. P. 1990 Virginia
Enns, W. R. 1960 Missouri
Epstein, M. E. 1994 District of Columbia.
Erwin, T. L. 1972 District of Columbia
Etnier, D. A. 1999 Tennessee
Evans, H. E. 1948 Colorado
Evans, W. G. 1957 (1994) Alberta
Evenhuis, N. L. 1980 Hawaii

Fairchild, G. B. 1939 Florida
Fales, J. H. 1944 Maryland
Fee, F. D. 1983 Pennsylvania
Feller, C. 1989 Maryland
Ferguson, D. C. 1969 District of Columbia
Fernandez, G. W. 1991 BRAZIL
Firko, M. J. 1994 Maryland
Fisher, E. M. 1977 California
Fisk, F. W. 1968 (1988) Florida
Fitzgerald, S. 1996 Colorado
Flint, O. S., Jr. 1961 District of Columbia
Flowers, R. W. 1994 Florida
Floyd, M. A. 1991 Kentucky
Fluno, J. A. 1957 Florida
Foote, B. A. 1958 Ohio
Foote, R. H. 1950 Virginia
Forattini, O. P. 1956 BRAZIL
Foster, G. A. 1999 Maryland
Fox, I. 1936 Puerto Rico
Franclemont, J. G. 1947 New York
Frank, J. H. 1994 Florida
Freidberg, A. 1979 ISRAEL
Freytag, P. H. 1979 Kentucky
Furth, D. G. 1994 District of Columbia

Gagné, R. J. 1966* District of Columbia
Gaimari, S. D. 1995 District of Columbia
Gates, M. 1998 California
Gelhaus, J. K. 1989 Pennsylvania
Gentry, J. W. 1958 Florida
Gibson, L. P. 1981 Ohio
Gimpel, W. F., Jr. 1995 Maryland
Glaser, J. D. 1988 Maryland
Goeden, R. D. 1982 California
Gomez-Arias, L. M. 1992 Florida
Gordon, R. D. 1968 North Dakota

Gordon, S.W. 1998 Maryland
Gorham, J. R. 1974 (1995) District of Columbia
Grace, J. K. 1987 Hawaii
Grissell, E. E. 1979 District of Columbia
Grogan, W. L. 1997 Maryland
Guang-Xue, Z 1999 P. R. OF CHINA
Ge-Xia, Q. 1999 P.R. OF CHINA

Haines, K. A. 1952 Virginia
Halbert, S. E. 1989 Florida
Hamilton, S. W. 1982 Tennessee
Hanks, L. M. 1993 California
Hanson, P. 1985 COSTA RICA
Hansson, C. 1985 SWEDEN
Harbach, R. E. 1972 UNITED KINGDOM
Harlan, H. J. 1988 Maryland
Harman, D. M. 1966 Maryland
Harrington, D. 1989 Texas
Harris, S. C. 1979 Pennsylvania
Harrison, B. A. 1976 North Carolina
Harrison, T. L. 1993 Illinois
Hastriter, M. W. 1998 Utah
Headrick, D. H. 1992 California
Henry, T. J. 1975 District of Columbia
Heppner, J. B. 1974 Florida
Heraty, J. M. 1986 California
Hespenheide, H.A., III 1981 California
Hevel, G. F. 1970 District of Columbia
Heydon, S. L. 1986 California
Hight, S. 1990 Maryland
Hilton, D. F. J. 1990* Quebec
Hill, R. E. 1997 California
HODGES, R. W. 1960* (1998) Oregon
Hoebeke, E. R. 1980 New York
Hoekstra, J. D. 1999 Illinois
Hoffmann, C. H. 1945 Maryland
Hoffman, K. M. 1986 South Carolina
Holzbach, J. E. 1984 Ohio
Holzenthal, R. W. 1997 Minnesota
Hopla, C. E. 1961 Oklahoma
Hoq, N. 1999 Maryland
Howden, H. F. 1948 Ontario
Huang, Y. -M. 1968 District of Columbia
Hung, A. C. F. 1981 Maryland
Hurd, L. E. 1988 Virginia
Husband, R. W. 1972 Michigan
Irwin, M. E. 1976 Illinois
Ivie, M. A. 1984 Montana

Jashenko, R. V. 1997 KAZAKSTAN
Jensen, A. S. 1997 Maryland
Jimenez, H. H. 1994 MEXICO
Johnson, E. L. 1995 Washington
Johnson, J. B. 1987 Idaho
Johnson, N. F. 1980 Ohio
Johnson, P. J. 1984 South Dakota
Joseph, S. R. 1957 Maryland
Judd, D. 1994 Oregon

Kane, M. 1999 Maryland
Kaster, C. H. 1979 Michigan
Keffer, S. L. 1993 Virginia
Keirans, J. E. 1984 Georgia
Kelley, K. C. 1998 Ohio
Kennedy, J. H. 1995 Texas
Kethley, J. B. 1974 Illinois
Kim, K. C. 1983 Pennsylvania
Kimsey, L. S. 1994 California
Kingsolver, J. 1963 (1992) Florida
Kirchner, R. F. 1981 West Virginia
Kitayama, C. 1974 California
Kittle, P. D. 1975 Alabama
Knutson, L. V. 1963* FRANCE
Kondratieff, B. C. 1992 Colorado
Konstantinov, A.S. 1997 District of Columbia
Korch, P. P. 1993 Pennsylvania
Kosztarab, M. 1978 (1994) Virginia
Kotrba, M. 1997 GERMANY
KROMBEIN, K. V. 1941* (1993) District of Columbia
Krysan, J. L. 1993 Kentucky

Labandeira, C. C. 1993 District of Columbia
Lago, P. K. 1984* Mississippi
Lakin, K. R. 1993 North Carolina
LaPierre, L. M. 1999 California
La Vigne, R. 1999 AUSTRALIA
Levesque, C. 1985 Quebec
Lewis, J. A. 1994 District of Columbia.
Lewis, P. A. 1974 Ohio
Lewis, R. E. 1958 Iowa
Li, C.-L. 1999 TAIWAN
Lien, J. C. 1967 TAIWAN

Lingafelter, S. W. 1997 District of Columbia
Lisowski, E. A. 1988 Washington
Little, R. G. 1993 California
Loechelt, H. K. 1988 Washington
Loeffler, C. C. 1992 Pennsylvania
Lyon, R. J. 1961 California

MacDonald, J. F. 1984 Indiana
MacKay, W. P. 1982 Texas
Magner, J. M. 1953 Missouri
Maier, C. T. 1976 Connecticut
Main, A. J., Jr. 1965 New York
Manglitz, G. R. 1956 (1989) Nebraska
Manley, D. G. 1984 South Carolina
Marsh, P. M. 1960 (1997) Kansas
Marshall, S. 1982 Ontario
Mason, H. C 1949 (1973) Maryland
Mason, S. 1999 Maryland
Masteller, E. C. 1995 Pennsylvania
Mastromatteo, L. 1999 District of Columbia
Mathis, W. N. 1976* District of Columbia
May, E. 1990 Kansas
McCabe, T. L. 1977 New York
McComb, C. W. 1956 Virginia
McDonald, F. J. D. 1983 AUSTRALIA
McGovran, E. R. 1937 (1973) Maryland
McKamey, S. H. 1989 District of Columbia
McKeever, S. 1990 Georgia
McPherson, J. E. 1985 Illinois
Mead, F. W. 1976 (1995) Florida
Mejdalani, G. 1996 BRAZIL
Menke, A. S. 1969 Arizona
Metzler, E.H. 1998 Ohio
Michener, C. D. 1994 Kansas
Miller, D. R. 1972 Maryland
Miller, G. L. 1981 Maryland
Miller, K. B. 1998 Colorado
Miller, R. S. 1981 Montana
Miller, S. E. 1980* Hawaii
Miller, T. D. 1988 Idaho
Mong-Luen, J. 1999 TAIWAN
Mitchell, R. T. 1949 (1978) Maryland
Munroe, E. 1986 Ontario
Moore, T. E. 1950 Michigan
Morales, I.M. 1998 MEXICO
Moran, M. D. 1994 Delaware
Morse, J. C. 1976 South Carolina
Moulton, J. K. 1994 Arizona
Moulton, S. R., II 1988 Colorado
Mullens, B. A. 1999 California
Muñoz-Quesada, F. 1996 Minnesota
Munroe, E. 1986 Ontario
Munson, S. C. 1938 (1975) District of Columbia

Nakahara, S. 1968 Maryland
Neff, S. E. 1969 Pennsylvania
Nelson, C. H. 1969 Tennessee
Neunzig, H. H. 1956 North Carolina
Norden, B. 1998 District of Columbia
Norrbom, A. L. 1989 District of Columbia
Novelo-Guiterrez, R. 1999 MEXICO
Nuhn, T. P. 1981 Virginia

Ochoa, R. 1999 Maryland
O'meara, G.F. 1999 Florida
Orr, R. L. 1990 Maryland
Oswald, J. D. 1987 Texas

Packauskas, R. J. 1993 Kansas
Painter, H. F. 1990 Virginia
Pakaluk, J. 1992* District of Columbia
Paras, F. 1999 Maryland
Paraskevoudakis, E. 1999 Maryland
Parker, C. R. 1977 Tennessee
Parrish, D. W. 1963 (1987) Maryland
Paulo, O. 1998 BRAZIL
Pedrosa-Macedo, J.H. 1999 BRAZIL
Peters, W.L. Florida
Peterson, R. V. 1952 Utah
Pike, K. 1995 Washington
Pinto, J. D. 1982 California
Plakidas, J. D. 1986 Maryland
Pogue, M. 1996 Maryland
Polhemus, D. A. 1993 District of Columbia
Polhemus, J. T. 1964 Colorado
Porter, C. H. 1984 Georgia
Pratt, H. D. 1943 Georgia
Pribyl, L.J. 1999 District of Columbia
Price, R. D. 1963 Arkansas
Pujolluz, J. R. 1998 BRAZIL
Pujol-Luz, C. V. de Assis 1998 BRAZIL
Pulawski, W. J. 1975 California

Quintero Arias, D. 1990 Florida

Rack, G. 1975 GERMANY
Rainwater, C. F. 1954 (1975) Maryland

Rainwater, H. I. 1964 (1983) Maryland
Ramsay, M. J. 1968 Maryland
Raspi, A. ITALY
Rawlins, J. F. 1974 Pennsylvania
Rayburn, B. S. 1998 Ohio
Reichart, C. V. 1946 Rhode Island
Revol, L. M. 1999 FRANCE
Ribeiro-Costa, C. S. 1992 BRAZIL
Richards, A. B. 1996 Colorado
Richardson, H. H. 1939 (1976) New Jersey
Rider, D. A. 1991 North Dakota
Riegel, G. T. 1952 Illinois
Riley, D. R. 1984 Texas
Robbins, R. G. 1979* Maryland
Robbins, R. K. 1986 District of Columbia
Robbins, T. O. 1989 Texas
Robinson, H. E. 1963 District of Columbia
Root, R. B. 1984 New York
Rothschild, M. J. 1989 Maryland
Roughley, R. E. 1992 Manitoba
Rozen, J. G., Jr. 1956 New York
Rueda, L. 1999 North Carolina
Ruiter, D. 1976 Colorado
Rumph, J. A. 1996 Washington
RUSSELL, L. M. 1930 (1988) Maryland

Sands, D. P. A. 1984 AUSTRALIA
Santana, F. J. 1966 Florida
Saugstad, E. S. 1979 Maryland
Scarbrough, A. G. 1971 Maryland
Schaefer, C. W. 1985 Connecticut
Schauff, M. E. 1980 District of Columbia
Schick, K. 1994 California
Schiff, N. M. 1991* Mississippi
Schmidt, C. H. 1969 North Dakota
Schmude, K. L. 1990 Wisconsin
Scudder, G. G. E. 1984 British Columbia
Sedlacek, J. D. 1988 Kentucky
Shaffer, J. C. 1974 Virginia
Shands, W. A. 1940 (1991) South Carolina
Sharkov, A. 1995 Ohio
Shaw, S. R. 1991 Wyoming
Shepard, W. D. 1992 California
Sheppard, W. S. 1995 Washington
Shinohara, A. 1981 JAPAN
Shorthouse, J. D. 1986 Ontario
Silva, V.C. 1999 BRAZIL
Sites, R. W. 1989 Missouri
Skelley, P. E. 1992 Florida
Slater, J. A. 1949 Connecticut
Sloan, M. J. 1983 (1990) District of Columbia
Smiley, R. L. 1964 Maryland
Smith, C. F. 1967 (1987) North Carolina
Smith, D. R. 1965* District of Columbia
Snelling, R. R. 1972 California
Solis, M. A. 1985* District of Columbia
Spangler, P. J. 1958* District of Columbia
Spilman, R. E. 1950 (1977) Maryland
Spinelli, G. R. 1983 ARGENTINA
Staines, C. L. 1975 Maryland
Staley, D. N. 1998 Kentucky
Starr, C. K. 1987 TRINIDAD & TOBAGO
Steck, G. J. 1988 Florida
Steinly, B. A. 1983 Ohio
Stewart, R. D. 1985 Maryland
Stibick, J. N. L. 1992* Maryland
Stoetzel, M. B. 1971 Maryland
Strickman, D. 1988 SOUTH KOREA
Surdick, R. F. 1979 Virginia
Sutherland, C. M. 1974 New Mexico
Sutherland, D. W. S. 1973* Maryland
Swearingen, J. M. 1999 District of Columbia
Swann, J. 1999 Ontario

Taft, S. 1999 Wisconsin
Tennessen, K. J. 1982 Alabama
Thomas, D. B. 1997 Texas
Thompson, F. C. 1968* District of Columbia
Thompson, J. V. 1953 (1985) New Jersey
Todd, R. G. 1993 Maryland
Togashi, I. 1983* JAPAN
Torres-Miller, L. R. 1984 West Virginia
Triplehorn, C. A. 1972 Ohio

Ulrich, H. 1978* GERMANY

Valley, K. 1976 Pennsylvania
Vazquez, A. W. 1957 Virginia
Vockeroth, J. R. 1995 Ontario
Voegtlin, D. 1981 Illinois

Wahl, D. B. 1987 Florida
Wallenmaier, T. E. 1979 Michigan
Waller, D. A. 1984 Virginia
Warren, A.D. 1999 Oregon

Webb, D. W. 1981 Illinois
Weber, N. A. 1941 (1981) Florida
Wenzel, R. L. 1984 Illinois
Wharton, R. A. 1981 Texas
Wheeler, A. G., Jr., 1974 South Carolina
White, G. B. 1977* Maryland
Whitsel, R. H. 1967 California
Whitworth, T. 1999 Washington
Will, K.W. 1997 New York
Williams, G. L. 1984 Maryland
Williams, H. B. 1977* District of Columbia
Williams, M. L. 1971 Alabama
Wilson, D. 1999 Mississippi
Wilson, N. 1957 Iowa
Wilterding, J. 1999 Michigan
Wojtowicz, J. A. 1981 Tennessee
Wood, D. M. 1987 Ontario
Wood, T. K. 1974 Delaware
Woodley, N. E. 1984* District of Columbia
Woolley, J. B. 1986 Texas

Yasunaga, T. 1998 JAPAN
Young, D. K. 1981 Wisconsin

Zack, R. 1982 Washington
Zimmerman, E. C. 1965 AUSTRALIA
Zolnerowich, G. 1987 Texas
Zuccaro, A. E., Jr. 1986 Mississippi
Zungoli, P. 1978 South Carolina
Zuparko, R. L. 1993 California

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Society Meetings

1,035th Regular Meeting—January 7, 1999

The 1,035th regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:38 pm by President-elect David Furth, stepping in for President Mike Schauff who could not attend. The meeting was held in the Waldo Schmidt Room of the National Museum of Natural History, Washington, D.C. Nineteen members and seventeen guests attended. The minutes from the 1,034th Regular Meeting were read and approved without modification.

Dave Furth asked for reports from the committees. Steve Lingafelter, Membership Chair, read the names of four new applicants for membership in ESW: Edgar A. Cohen, Jr., Jon D. Hoekstra, Pat Durkirs, and Leo Mastromatteo.

With eight member proxy votes carried by Dave Furth, quorum was reached and voting was held on the three proposed amendments to the ESW bylaws and nominations of Dr. Louise M. Russell and Dr. Ronald W. Hodges for new Honorary President and new Honorary Member, respectively. The amendments and proxy votes are attached. After all attempts at new discussion on the proposed amendments were successfully quashed, voting was held on each amendment and all passed with a majority vote.

Five visitors were introduced.

Bill Bickley noted that Dr. William H. Anderson, former ESW President and USDA coleopterist, died in 1997. Dave Furth announced that a très spiffy beetle calendar from the American Museum of Natural History is available and had one on display.

Dave Furth finally relented the podium after introducing the evening's speaker, Past President Warren Steiner, who described his role in last year's "Navassa Island Bio-Blitz." The Department of the Interior recently acquired this 5.2 square km, little known island between Haiti, Cuba and Jamaica. The Center for Marine Conservation organized an expedition to inventory Navassa's biodiversity and other natural resources. Warren Steiner and Jil Swearingen were responsible for surveying the terrestrial invertebrates, as part of an elite force of botanists, geologists, and vertebrate biologists who had been granted "unconditional, unfettered and unqualified permission" by the Office of Insular Affairs to collect scientific samples. From July 24 to August 5, 1997, they traversed the unexpectedly rich array of habitats on this unwelcoming land of rugged, pitted limestone, escaping with only minor cuts, moderate poisonwood rash, and lots of specimens. They used Malaise traps with flight intercept pans, sets of pitfall traps, yellow pan traps, black lights, and various manual methods to sample leaf litter, soil, rotten wood, fungi, foliage, air, and water. Plant-associated insects were unexpectedly speciose and include some widespread Caribbean species. Soil faunas included flightless beetles but were not as rich as expected, probably due to the historical difficulty in colonizing an island surrounded by high vertical cliffs and no beach.

Steiner and Swearingen reaped many species: at least 130 species of Coleoptera, 87 of Diptera, 24 of ants, 75 of other Hymenoptera, 104 of Lepidoptera (including 10 butterfly species), about 120 of other insect orders, and 108 non-insect arthropod species (mostly spiders). Of the more than 500 species found, all except one spider represent new records at least. Extrapolating from a few selected taxa, they estimate that 30 percent of the species may be new species endemic to Navassa—with more species still to discover.

The meeting was adjourned at 9:10 pm. Refreshments were generously provided by Gabriela Chavarría, who could not attend.

Respectfully submitted,
Stuart H. McKamey
Recording Secretary

1,036th Regular Meeting—February 11, 1999

The 1,036th regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:33 pm by President Michael Schauff in the Waldo Schmidt Room of the National Museum of Natural History, Washington, D.C. Twenty members and eight guests attended. The minutes from the 1,035th Regular Meeting were read and approved with minor modification.

Mike Schauff asked for reports from the committees. Steve Lingafelter, Membership Chair, read the names of five new applicants for membership in ESW: Frederick Paraskevoudakis, Robert Lavigne, Stephanie Mason, Louis J. Pribyl, and A. Dan Wilson. New applicant Louis Pribyl, interested in fossil insects, was introduced. Five visitors were also introduced.

As exhibits, Dave Furth displayed an enlarged sheet of U.S. postal stamps with illustrations of insects, to be issued in October, 1999. The Smithsonian, and particularly Gary Hevel, had a hand in developing them. Dave Smith, editor of the *Proceedings*, displayed ESW's recently published, 287-page Memoir 22: Systematics of North American Trichogrammatidae. Mike Schauff noted that the National Museum holds the holotype of the smallest insect ever described, measuring in at 140 microns.

Dave Furth introduced the evening's speaker, Alan Schroeder of the U.S. Agency for International Development. He presented an overview of the "U.S. AID's Pest Management Activities in Africa." The agency has two main programs: collaborative research on Integrated Pest Management and the locust program. The IPM program focuses mostly on subsistence crops in Mali, Eritrea, and Uganda and emphasizes training and education. The locust and grasshopper program provides training, monitoring, and emergency assistance. The four species of migratory locusts are easiest to control before their populations reach threshold sizes. The brown locust, for example, has been kept below migratory levels through control efforts and is now mostly limited to South Africa. However, control efforts on the other species are hampered by breeding grounds that are remote, by unpreparedness, and the presence of armed conflict. The last major plague was 1986–1989, with swarms literally covering up to 1,000 square kilometers and traveling 100 km per day. The price tag: $300,000,000 in pesticides sprayed over 25 million square kilometers in 28 countries. Nevertheless, it is thought that the end of the plague was due to a change in natural weather, which is considerably cheaper. Excessive aid for controlling past locust plagues have resulted in a huge build-up of obsolete pesticides, to the tune of 71,000 metric tons. Spillage, poor storage, rusted containers, and misuse, such as using containers to carry water or to build toys, are common and frequently result in human sickness and death. Additional toxins reach humans through the food chain indirectly and directly, as immatures and adults are commonly eaten and even sold in markets. Working through the United Nations' FAO with other donors, U.S. AID has successfully implemented training and educational programs, convinced donors to reduce pesticide build-up by sending smaller, more frequent shipments, coordinated international exchange of excess pesticides, and funded IPM work focusing on entomophagous fungi. However, the end of locust plagues is not in sight.

The meeting was adjourned at 9:00 pm. Refreshments were provided by John Brown.

Respectfully submitted,
Stuart H. McKamey
Recording Secretary

1,037th Regular Meeting—March 4, 1999

The 1,037th regular meeting of the Entomological Society of Washington (ESW) was called to order at 7:30 pm by President Michael Schauff in the Waldo Schmidt Room of the National Museum of Natural History, Washington, D.C. Twenty members and 16 guests attended. The minutes from the 1,036th Regular Meeting were read and approved without modification.

Mike Schauff asked for reports from the committees. Steve Lingafelter, Membership Chair, read the names of the only new applicant for membership in ESW: Andrew Warren. New member Pat Durkins was introduced. Fourteen visitors were also introduced.

For exhibits, Mike Schauff had the holotype of smallest insect ever described (140 microns), a male mymarid wasp, parasitic on psocid eggs, under a microscope. Dave Furth displayed a 2-volume publication in English: Handbuch der Zoologie; the first volume is a dictionary of insect morphology and the second is on Lepidoptera, with many Smithsonian and USDA systematists as contributors. Gene Rosenberg (Botanical Society of Washington) invited attendees to participate in upcoming field trips to Bear Island on April 3rd and 10th, and announced two upcoming speakers in the D.C. area.

Dave Furth introduced the evening's speaker, Dale F. Schweitzer of the New Jersey branch of the Nature Conservancy. Schweitzer described the "Lepidoptera and Other Insects in the New Jersey Pine Barrens." At the end of the day, however, no other insects were mentioned. Pine barrens generally consist of scrawny pines, scrubby oaks, a lower ericaceous heath layer, and grassy patches over white sand. Usually managed by fire, Schweitzer described the great variety of pine barren habitats at different elevations, soil water conditions, and fire management practices. For example, if wet, with too much fire, a pine barren resembles a bog. With 1,024 macrolepidoptera, the NJ pine barrens are moderately diverse. Their noteworthiness derives more from their biogeographic importance, being the northern limits of about 30 southern Lepidoptera species and the southern limit of about 32 northern species. They contain four endemics, which is unusually high given the recent glaciation of the Northeast U.S. They contain several undescribed species as well. The moth disjunctions seem to result from a combination of host plant and white sand habitat, as many of the hosts have a wider distribution than the moths. The NJ pine barrens hold several dozen globally rare species. Few species have been lost so far, but some are on the decline because of changes in fire practices.

The meeting was adjourned at 9:00 pm. Refreshments were provided by Michael Schauff.

Respectfully submitted,
Stuart H. McKamey
Recording Secretary

1,038th Regular Meeting—April 1, 1999

The 1,038th regular meeting of the Entomological Society of Washington was convened on April Fool's Day 1999—same place, same time, same station. President Michael Schauff again called the meeting to order without the gavel, begging the question, "Where is that gavel?" Could it be that Schauff has lost this vital and priceless society heirloom? Actually, I think you can buy a new one for about $5.00, but I digress. The meeting was well attended, with 19 members and 14 guests present; 5 of the latter were introduced. John Brown, pinch-hitting for Stu McKamey, stumbled through the minutes, which were approved with minor modifications.

Mike Schauff asked for reports from the committees. In Steve Lingafelter's absence, there was no reading of new applicants for membership.

The show-and-tell portion of the meeting included sawflies, insect kite-flying (from the Smithsonian Magazine), an insect um-

brella (material with insect pictures—not for use by insects), two entomology books, and announcements of Bugfest and the Big Move. Schauff solicited a volunteer for a new society position—Refreshment Chair. There were no immediate takers.

Dave Furth introduced the evening's speaker, Dr. Ted R. Schultz of the Department of Entomology, Smithsonian Institution. [I suspect Ted received no travel honorarium to get to the meeting.] The title of Ted's talk was "The Natural History of Fungus-Growing Ants." The presentation included an introduction to the historical literature on fungus-growing ants, a milestone of which was the hypothesis in 1874 by Thomas Belt that the ants were cultivating fungus for food. Then Ted described and illustrated different types of nests and fungus-growing activities. He indicated that the tribe Attini, which includes all the fungus-growing ants, is restricted to the New World, primarily the Neotropics, and is comprised of about 210 described species. Ted presented information on the phylogenetics of both the ants and the associated fungi, which strongly supported the monophyly of fungus-feeding, but showed limited support for true coevolutionary patterns. Ted closed with the conclusion that ant "agriculture" is much like that of human agriculture, with shifts and changes taking place through space and time in response to environmental factors. The talk was followed by a lively question and answer period.

The meeting was adjourned at 8:55 pm. Refreshments were provided by Mike Schauff.

Submitted by
John W. Brown
Pinch-Hitting Secretary

1,039th Regular Meeting—May 6, 1999

The 1,039th regular meeting of the Entomological Society of Washington (ESW) was called to order in the Waldo Schmidt room of the National Museum of Natural History, Washington, D.C., by President Michael Schauff at 7:35 pm. The meeting was attended by 16 members and 2 guests, who were introduced. Stu McKamey read the minutes of the 1,038th meeting, which were approved without modification. Guest Michael Mungai, from the Kenya National Museum, was introduced.

Mike Schauff asked for reports from the committees. Steve Lingafelter read the names of five new applicants for membership: Rodolfo Novelo-Gutiérrez, Kieran M. Clements, Mike Arduser, Larry E. Morse, and Mary Liz Jameson.

The first order of business was the nomination of honorary members Bill Buckley and Don Anderson. The nominations were accepted and approved by unanimous vote. President Schauff mentioned the ESW Annual Banquet coming up on June 24th at the Uniformed Services University of Health Sciences in Bethesda, MD.

For exhibits, Chris Thompson displayed the first purely digital scientific journal, the Diptera Data Dissemination Disk, which is the official journal of the North American Dipterists Society and which includes copies of two other publications. Dave Furth announced the May 15 Bugfest public event on the Mall, an insect morphology T-shirt, and a variety of stunning beetle slides taken by National Geographic photographer Mark Moffet. Ed Saugstad passed on his awareness of a Threatened Fritallaries Officer in the United Kingdom, and Mike Schauff mentioned the recently opened IMAX theater and cafeteria at the Natural History building.

Dave Furth introduced the night's speaker, Joseph V. McHugh of the University of Georgia, who presented his research on the "Phylogeny of Erotylidae with implications for the Evolution of Mycophagy." There are about 2,500 species of pleasing fungus beetles known. Many are likely models in mimicry complexes with tenebrionids, cassidine leaf beetles, etc. Many are gregarious and some exhibit parental care. Like most fungus-eaters, erotylids are generally po-

lyphagous, presumably because of the unpredictability of resources. Through his work in the tropics studying and rearing erotylids, Dr. McHugh has discovered a general restriction to fungus orders and that species are more selective in their breeding hosts than in their nibbling or eating hosts. Mapping host use on his estimate of erotylid phylogeny, he proposed that, contrary to the stereotypical pattern of evolution through overcoming barriers or constraints followed by radiation, erotylids may provide an example of radiation with increasing host specificity.

The meeting was adjourned at 9:00 pm sharp. Refreshments were provided by John Brown, assuming this new responsibility of Program Chair.

Respectfully submitted,
Stuart H. McKamey
Recording Secretary

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100 Years Ago

The following minutes of the November 2, 1899 meeting of the Entomological Society of Washington are from the *Proceedings of the Entomological Society of Washington,* Volume IV, No. 4 (January 12, 1899, to December 6, 1900) [Issued July 16, 1901.]:

"November 2, 1899.

The 146th regular meeting was held at the residence of Mr. C. L. Marlatt, 1440 Massachusetts ave. President Gill in the chair, and Messrs. Johnson, Dyar, Motter, Ashmead, Caudell, Busk, Vaughan, Schwarz, Marlatt, Heidemann, Uhler, Benton, Patten, Howard, and Currie, active members, and Kotinsky and Stetson, visitors present.

Mr. Schwarz announced the death of Mr. Hugo Soltau, a corresponding member, and the further fact that by Mr. Soltau's will his extensive collection of Coleoptera was bequeathed to the National Museum.

Under the head of Exhibition of Specimens and Short Notes, Mr. Ashmead showed an insect constituting a new genus of Bethyllidae collected in Arizona by Mr. Schwarz. He also exhibited specimens of *Dinoura* (n.g.) *auriventris* n. sp. and *D. cyanea* n. sp, which he had recently received from Mr. W. W. Froggatt, of New South Wales, who had reared them from galls of Coccids of the Brachyscelid group. The insects belong the family Cleonymidae, all the species of which are parasitic upon coleopterous larvae, so that these Dinouras are probably parasitic upon coleopterous larvae, feeding in the Brachyscelid galls. Mr. Schwarz said that in Europe there is an Anthribid beetle belonging to the genus Brachytarsus, which is a specific enemy of Lecanium scales; this genus is represented in Australia, and it is quite likely that one of its species is the true host of the Dinoura.

—Mr. Marlatt showed photomicrographs of the anal plate of a number of Diaspine scales. He showed both bromide prints and platinotypes, the former being better. From the results so far obtained, he believes that this will be an excellent method of illustrating or at least studying the obscure features of the anal plates of Coccidae.

—Prof. Uhler exhibited specimens of certain Capsids, of which the females only had been previously known. They were, *Coquillettia insignis* Uhler, *C. amoena* Uhler, *Lobitodes integer* n. sp., *Myrmicides polita* n. sp., and *Orectoderus obliquus* n. sp., the males of these interesting forms having recently been found by Mr. Elmer D. Ball in Colorado inhabiting ants' nests. They were entirely different from the females, being wingless and resembling ants so closely in general appearance that it is a

plain case of protective mimicry. In answer to a question, he said that we have now about 2,000 species of the family Capsidae in America north of Mexico, but that many of the forms extend well down into South America. Mr. Ashmead spoke of the occurrence of winged and wingless forms in Hymenoptera as generally associated with dimorphism and frequently with alternation of generations. Mr. Uhler said that this could hardly be the case with the Capsids, for here we have a distinct gradation of wing length. Mr. Ashmead said that he had a species of Scollops from Oregon showing an apparent dimorphism, but Mr. Uhler thought that the form might have belonged to one or more of several allied genera erected by Stal. Mr. Ashmead said that a point like this could only be settled by careful outdoor observations; the systematist working over a collection of insects is apt to lose true relationships, which can be established to the best advantage by field observations. Apropos to this remark, Mr. Howard mentioned the figure published in a recent number of the British Medical Journal as illustrating the difference between Anopheles and Culex in the resting position.

—Mr. Heidemann exhibed a Capsid, *Eccritotarsus elegans* Uhler, which had been found by Mr. Banks at Falls Church, Va., on *Euphorbia adenoptera.* Mr. Heidemann had also found it upon the same plant at Columbia Heights, D.C., and thinks that the Euphorbia is its food plant. The insect was originally described by Prof. Uhler from Illinois, and Mr. Heidemann has also taken it at Round Hill, Va. Mr. Ashmead said that he had seen the same insect from Texas. Mr. Schwarz called attention to the fact that the food plant is a native of South America, and Mr. Uhler remarked that Eccritotarsus is really a South American genus, some 30 species being known from that continent; in his own collection he has *E. elegans* from Boston and Texas, and a large series from Galesburg, Ill. The genus is remarkable in having only one loop in the membrane of the wing cover, and it has a greater width of curve than is usually found in the Capsidae. Mr. Howard asked the faunistic value of the Capsidae as a group, and Mr. Uhler said that they had not been carefully enough collected to enable him to judge of this point, and made some interesting remarks about collecting Capsidae, crediting Mr. Heidemann and Mr. Elmer D. Ball with great success in this difficult task.

—The first paper of the evening was by Dr. Dyar, and was entitled: [follows paper by Dyar and several others read at the meeting, with comments and questions from those present].''

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