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NEOTROPICAL MICROLEPIDOPTERA XXIII. FIRST REPORT OF THE FAMILY ERIOCOTTIDAE FROM THE NEW WORLD, WITH DESCRIPTIONS OF NEW TAXA

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Abstract.—*Crepidochares subtigrina* Meyrick from Brazil is redescribed and transferred to Eriocottidae. Formerly this monotypic genus and species had been included in Tineidae. In addition, four new species of ***Crepidochares***, ***C. aridula*** and ***C. austrina*** from Chile, ***C. colombiae*** from Colombia, and ***C. neblinae*** from Venezuela are described for the first time. The discovery of these taxa marks the first record of the primitive tineoid family Eriocottidae for the New World. Supplemented by numerous illustrations, the morphology of these and related Old World taxa are summarized.

Key Words: Lepidoptera, Eriocottidae, *Crepidochares*, biogeography

Recent investigations on the tineoid complex by the author together with an earlier study by Nielsen (1978) have shown the predominantly Old World family Eriocottidae to be among the most ancient of the ditrysian Lepidoptera. Because the Eriocottidae are the only ditrysian moths known to possess microtrichia randomly scattered over all wing surfaces, I consider this family to be the most primitive member of the Tineoidea. More importantly, this implies that among the extant Lepidoptera, they most resemble the stem ancestor of the Ditrysia.

Prior to this paper, no Eriocottidae were reported to occur in the New World. An eriocottid, *Crepidochares subtigrina*, was previously described by Meyrick (1922) from the Amazon, but this species had been regarded as a tineid. Fieldwork in southern Chile by the author, R. E. Brown, O. Karsholt, and E. S. Nielsen in 1981 resulted in collections of two new species. A recent multidisciplinary biological survey of Cerro de la Neblina in Venezuela produced another undescribed species. The latter appears to be a sister species of yet another new montane species from Sierra del Libano, Colombia, thus bringing the total species of Eriocottidae known for South America to five. To supplement the descriptions of the new American taxa, a brief review of the biology and morphology of the family is provided.

Depositions of specimens referred to in this paper are: ANIC for Australian National Insect Collection, CSIRO, Canberra, Australia; BMNH, British Museum (Natural History), London, England; NHNS, Museo Nacional de Historia Natural, Santiago, Chile; USNM, National Museum of Natural History (formerly the United States National Museum), Smithsonian Institution, Washington, D.C.; UCVM, Universidad Central de Venezuela, Maracay, Venezuela; and ZMUC, Zoologisk Museum, Universitets Kobenhaven, Copenhagen, Denmark.

BIOLOGY

Distribution.—Prior to this report, the Eriocottidae as reconstituted by Nielsen (1978), were known to occur only in the Old

Map 1. Distibution of *Crepidochares* in northern South America.

World. The genus *Eriocottis* ranges from southern Europe (Spain, Italy), northern Africa (Algeria), southern USSR, Asia Minor to Taiwan. I have examined the Taiwanese species, *Eriocottis flavicephalana* Issiki (Figs. 8, 115–119), and found it to agree in all respects to *E. fuscanella* Zeller, with the notable exception that the maxillary palpi are five segmented and the ocelli are reduced (thus agreeing with Issiki's (1930) original description). Another recognized genus of the subfamily Eriocottinae, *Deuterotinea*, is believed to be less widely distributed and confined largely to southern Europe and Asia Minor, from Spain eastward to Syria, Israel, Iraq and southern USSR. A single genus and species of Eriocottinae, *Eucryptogona trichobathra* Lower, occurs in New South Wales, Australia (Nielsen, in litt.).

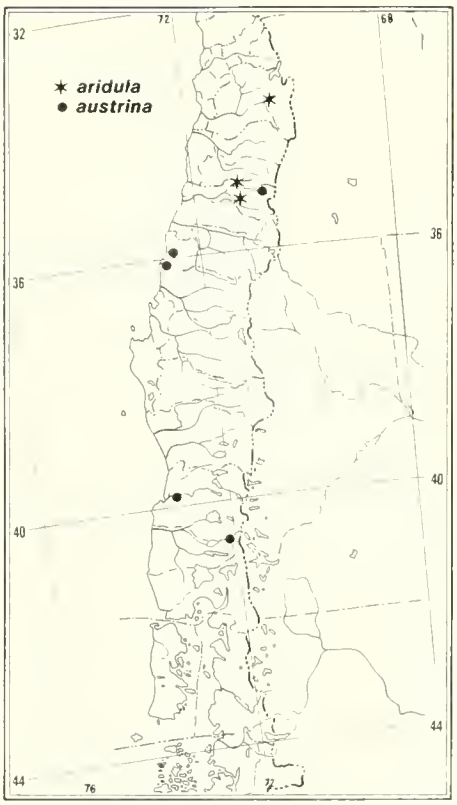
In the New World, Eriocottidae are restricted to South America where two genera are recognized, both allied to *Eriocottis*. Thus far, most of the South American species have been found only in temperate forests or high elevations (Maps 1, 2). *Crepidochares subtigrina*, however, was collected at Parintins along the Amazon River, which suggests the existence of more species through the vast neotropical lowlands. In 1981 I collected two, very distinct species of Eriocottinae in two different biotic regions of Chile (Map 2). *Crepidochares aridula*, new species, was found only in the drier, more northern, Central Valley and environs, whereas *Crepidochares austrina*, new species, was collected at several localities in the wetter, *Nothofagus* dominant, Valdivian forests to the south (see Davis, 1986,

Map 2, for limits of biotic regions). At approximately the same time, Nielsen and Karsholt collected *C. austrina* near Valdivia and Anticura, Chile.

Compsoctena, the largest genus and sole representative of the Old World subfamily Compsoctenidae, appears the most diversified through the Ethiopian Region (sub-Saharan Africa), where a majority of the known species occur, with numerous species also reported from India to mainland China and Taiwan and through portions of Indonesia. As shown by Dierl (1970), most of the known species of *Compsoctena* were proposed in other genera, often in *Melasina* or in genera now synonymized under *Compsoctena*. Several of these species are yet to be studied and still reside in their original genus. One such species, *Alavona thaitesii* Walsingham, has been examined in this study and transferred to *Compsoctena*.

Life history.—As is true for most families of moths, one of the most pressing needs for fieldwork among the Eriocottidae is for studies on life history and the immature stages. As pointed out by Nielsen (1978), little is known of their biology. Apparently few members of Eriocottidae have been reared, and their larval habits have largely been speculated (e.g. possibly feeding in decayed wood, leaves, or as stemborers). Adults appear to be univoltine and are active in the spring, both in the northern and southern hemispheres. Adult females of the middle eastern, steppe inhabiting *Deuterotinea* are wingless. Their larvae are detritophagous and construct silken tunnels often with ventilation tubes amongst grass litter (Zagulayev 1973, 1988). All specimens of *Crepidochares* collected by me were taken in ultraviolet light traps. The general structure of their highly extensible ovipositors indicates that the eggs are inserted into crevices within the host substrate.

Only slightly more is known about the habits of Compsocteninae. Dierl (1970) provides some evidence that the larvae live underground in silk and earthern tubes, or



Map 2. Distribution of *Crepidochares* in Chile.

(as may be true for *Compsoctena reductella* (Walker)) bore into decaying plants such as *Artemisia* and *Rubus*.

Morphology

The major morphological features of Eriocottidae, as they relate to systematics, have been summarized by Dierl (1970) and Nielsen (1978). As discussed by these authors, the principal synapomorphy of the family is the presence of a fourth pair of short, anterior apophyses located dorsally within the eighth segment of the female abdomen. In the subfamily Eriocottinae these are mostly fused in an X-shaped configuration (Figs. 121, 127, 130). The dorsal anterior apophyses may be either X-shaped or separate in *Compsoctena*. The new Chilean species, *Crepidochares aridula*, is unique in

possessing a fifth pair of ventral apophyses (Fig. 130) within the eighth segment in addition to the fourth, X-shaped, dorsal pair. No other species of Lepidoptera is known to have developed this many pairs of abdominal apophyses.

The Compsocteninae are easily distinguished from Eriocottinae in being generally larger, without ocelli, with greatly reduced, two segmented maxillary palpi and a minute haustellum (Figs. 20–21). Furthermore, the male antenna is shortly bipectinate in Compsocteninae, compared to simple in female *Compsoctena* and in both sexes of Eriocottinae. The antenna of male *Crepidochares subtigrina* is unusual in possessing two ventral pairs of short tubercles bearing elongate sensilla chaetica (Figs. 58–60). This relatively aberrant species also has lost the ocelli, and possesses reduced, three segmented maxillary palpi and porrect labial palpi (Figs. 14, 15), similar to the Australian *Eucryptogona trichobathra*. According to Nielsen (in litt.), the latter differs from *Crepidochares subtigrina* in possessing more slender wings, flagellomeres without lobes, and male valvae more similar to *Eriocottis*. Although Nielsen described the antennal pecten as absent in *Eriocottis*, I have found it present in all genera, although sometimes less distinct in *Compsoctena*. The presence of an antennal pecten is the plesiomorphic condition in Tineoidea as well as the non-ditrysian moths.

The wings of Eriocottidae are unique among the ditrysian moths in retaining microtrichia randomly scattered over all wing surfaces. This resembles the plesiomorphic condition present in nearly all non-ditrysian families. In Eriocottidae the microtrichia are relatively short and sparsely distributed (Figs. 26, 27, 44, 48–50, 64, 70, 72), with some variation to be noted. In at least one species, *Eriocottis fuscanella* Zeller, microtrichia are largely absent from the dorsal surface of the hindwing and restricted mainly to the wing base. Microtrichia have been lost over nearly all of the wing surfaces in all other Ditrysia, with the notable exception of the tineid genus *Eudarcia*, where they are absent only over the dorsal surface of the forewings. The possibility exists for microtrichia to be even more developed in other Tineidae not yet examined. If such a condition were found, then this would necessitate a re-evaluation of the supposed basal position of the Eriocottidae among the Ditrysia.

The male retinaculum was similar in all genera examined in consisting of an elongate, flaplike fold from the ventral costal margin and extending over the base of Sc (Figs. 24, 46, 47, 66–68). The outer margin of the retinaculum in *Crepidochares aridula* (Figs. 46, 47) appears more revolute than in *Eriocottis* or *Compsoctena*. In addition to sharing a similar, plesiomorphic retention of wing microtrichia, *Eudarcia* also possesses a male retinaculum similar to that of Eriocottidae. The retinacula of 7 other tineid genera examined, representing major subfamilies, were found to resemble the more typical ditrysian type (Davis, in press) consisting of a slender cuticular lobe arising from the underside of the subcostal vein. Although the male retinacular lobe arises slightly anterior to Sc in other tineoids and apparently in most ditrysian families, in some genera (e.g., *Atteva*) it originates on Sc as in the Tineidae examined. The curled apex of the lobe forms a short tube for firmly clasping the male frenulum. As is true in the case with microtrichia, too few tineid genera have been examined to determine the systematic significance between the subcostal costal fold (*Eudarcia*, Eriocottidae) and the curled subcostal lobe types (most Tineoidea and higher Ditrysia). Both types of male retinacula occur within the subdivision Monotrysia, as well as within a single family (Palaephatidae, Davis 1986, Psychidae). Studies to date indicate the subcostal costal fold type to represent the plesiomorphic state. Although *Eudarcia* displays

certain plesiomorphic similarities to Eriocottidae, no female *Eudarcia* examined to date has been observed to possess a fourth pair of abdominal apophyses. Consequently, this genus has not been included within Eriocottidae.

The mesofurcasterna of Eriocottidae are similiar in possessing relatively broad, stout, secondary arms (Figs. 88, 92). The apices of the secondary arms differ in *Compsoctena* in having the lateral branch reduced to a small tubercule with an attached tendon (Fig. 92) and in the greater elongation of the mesal branch. The metafurcasterna of the various genera are also of similar morphology, with the furcal apophyses of *Compsoctena* more attenuated (Figs. 93, 94). The apices of the metafurcal apophyses of *Crepidochares aridula* and *C. austrina* are truncate, with those of other *Crepidochares* and *Eriocottis* being somewhat intermediate in development (Fig. 91).

If the examples studied are typical of their respective subfamilies, then the Eriocottinae and Compsocteninae may also differ in leg structure. The pretarsal unguitractor plates of *Crepidochares neblinae* and *C. aridula* are less developed with only two to three ranks of scutes per transverse row (Figs. 33, 57). As is typically the condition in large moths, the unguitractor plate of *Compsoctena thwaitesii* (Walsingham), new combination, is larger and with a much greater number of scutes (8 to 12 ranks, Fig. 75). Apparently what often occurs in this, as well as in other families I have examined, is that as the plate enlarges or decreases with body size, the relative size of the scutes does not change proportionally but individual scutes are added or lost in number to cover the appropriate area. A more significant difference between the two groups may involve the epiphysis, which is lost in some species (Nielsen 1978). The epiphysis of *Crepidochares* (Figs. 29–31, 52–55), and *Eriocottis* are of the standard form, with a comb (or pecten) of stout spines along the inner, cleaning edge and covered elsewhere with tightly appressed, imbricated, scale-like spines. In *Compsoctena thwaitesii* (Figs. 78–81) the epiphysis is more elongate and more specialized in lacking both pecten and imbricated spines. The stiff, tibial scales normally opposite an epiphysis also appear to be lacking in this species. The apex is slightly broadened and, similar to all other surfaces of the epiphysis, densely covered with deciduous scales. The only spines present are minute in size and scattered along the anterior surface (Fig. 81).

The two principal morphological systems probably used most frequently in Lepidoptera systematics, wing venation and male genitalia, appear relatively conservative among Eriocottidae. Wing venation varies little among all known genera, with no stalked or branched veins present and with R5 terminating at or slightly above the apex of the forewing. The male genitalia appear rather uniform within genera (as is typical for another tineoid family, Psychidae), with a prominent spinose lobe arising from either the ventral margin of the cucullus in the Old World genera (and in many Psychidae), or from the distal margin of the sacculus in the only recognized Neotropical genus, *Crepidochares*. The male genitalia of the latter exhibit greater morphological differences between species than is generally true for other eriocottid genera, particularly with regard to the development of the spinose, saccular lobe.

Crepidochares Meyrick

Crepidochares Meyrick, 1922: 601.—Fletcher, 1929: 58.—Clarke, 1970: 36.—Davis, 1984: 4, 21.

Type species.—*Crepidochares subtigrina* Meyrick, 1922; by monotypy.

Adult.—Small, pale yellowish to brown moths with forewings variably and often indistinctly banded with brown to fuscous. Ocellus usually present; maxillary palpus 3–

5 segmented; labial palpus porrect or upcurved. Male valva with a spinose process from sacculus. Female genitalia with usually four pairs of apophyses or five pairs in *C. aridula*. Length of forewing 4.6–9.5 mm.

Head: Vestiture rough, consisting of long piliform scales with simple, acute apices. Antenna usually filiform, with two pairs of ventral tubercles per segment in *C. subtigrina*, 0.4–0.7 the length of forewing, 31–40 segmented; scape with pecten of 6–10 piliform scales; flagellum usually with dorsal half covered with moderately broad scales, ventral half naked except for dense sensilla, completely encircled by scales in *C. neblinae*. Eye round, relatively well developed; interocular index ranging from 0.63–1.1; eye index 0.73–0.92. Ocellus usually present, absent in *C. subtigrina*. Chaetosemata absent. Pilifers (Fig. 37) well developed, bearing 7–8 elongate bristles directed mesally and nearly touching at midline. Mandible either vestigial or absent. Maxillary palpus usually 5-segmented and equalling or slightly longer but more slender than labial palpus and about half the length of haustellum; basal three segments the shortest and apical two the longest and approximately equal in length; maxillary palpus less than one fifth the length of labial palpus and composed of three short segments in *C. subtigrina*. Haustellum elongate, often twice the length of labial palpus; distal half to two thirds externally covered with short overlapping plates (Fig. 40). Labial palpus 3-segmented, moderately well developed, usually slightly upcurved (Fig. 13) with subapical sensory pit reduced (Figs. 42, 43); palpus larger, relatively smooth and porrect in *C. subtigrina* (Figs. 14, 15).

Thorax: Forewing moderately slender; length 3–3.6 the width. Radius 5-branched; all veins arising separate; R5 usually terminating just before apex, or at apex (in *C. subtigrina*); R1 arising usually from basal third of discal cell, or mesad (in *C. austrina*). Media 3-branched, all veins separate. Discal cell 0.55–0.63 the length of forewing. Accessory and intercalary cells usually developed. 1A and 2A separate at basal 0.3–0.4, forming an anal loop. Retinaculum of male composed of a broad fold arising immediately under costal margin and partially extending over base of Sc (Figs. 24, 46, 47); retinacular fold absent in female, instead retinaculum consisting of a row of elongate, piliform scales from base of Sc. Microtrichia generally distributed over all wing surfaces in *C. neblinae*, most concentrated over basal half of discal cell or underside of forewing in *C. aridula*, not examined closely in other species. Hindwing nearly as broad as forewing, length 2.2–2.8 the width. All veins arising separate; base of M usually forked within cell, rarely entire. Frenulum single in male (Fig. 51), 2–4 bristles in female. Foreleg with pectinated epiphysis (Figs. 29–31, 52–55) approximately 0.4 the length of tibia; outer surface covered with flat, moderately broad, imbricate spines (Figs. 31, 55). Midleg with an elongate, apical pair of tibial spurs of unequal length. Hindleg with two pairs of elongate tibial spurs of unequal length, one pair apical and other pair arising from outer ⅗; basal tarsomere with row of 6–8 small spinose setae and apices of all tarsomeres with 3 small setae. Prothorax (Fig. 86) with sternum moderately developed, lightly sclerotized on either side of basisternum; patagium greatly reduced, nearly touching opposite member at dorsal midline; scutum greatly reduced, triangular, tapering to form slender, poorly differentiated scutellum. Mesothorax (Fig. 88) with secondary arms of furcasternum relatively broad and stout, abruptly terminating in a pair of short, acute processes; forked ends of secondary arms widely spaced, a distance about equal to width of mesothoracic phragma. Metafurcasternum (Fig. 90) with a pair of stout, either truncate or attenuate furcal arms, each with a single tendon directed anteriorly from anterior apex.

Abdomen: Relatively simple, without specialized process, coremata, or corethrogyne. Second sternum of tineoid type, with

a pair of slender apodemes projecting anteriorly from sternum; a minute tubercule and tubercular plate immediately laterad to base of apodeme.

Male genitalia: Uncus divided into two short, acute lobes, otherwise not differentiated from relatively broad, hoodlike tegumen. Vinculum moderately short, either V-shaped or attenuated into a distinct saccus. A more or less sclerotized, plate like subscaphium sometimes present which is fused medially to slender U- or V-shaped gnathos. Juxta and socii absent. Valva with basal half (sacculus) moderately broad, either equal to or twice the width of usually more slender distal half; (cucullus); ventral margin of cucullus without prominent spinose lobe (pollex) but with a variably developed spinose lobe from distal margin of saccular lobe; lobe largest in *C. neblinae*, most reduced in *C. aridula*. Aedoeagus relatively slender, short, without cornuti; phallobase well developed, nearly twice the length of aedoeagus and enclosing distal part of ejaculatory duct.

Female genitalia: Ovipositor greatly elongated, telescoping, with usually four or rarely five pairs of rodlike apophyses; posterior pair the longest, extending from A7 to caudal apex of abdomen (A10); a much shorter ventral pair located entirely within A10; anterior pair elongate and extending caudad into A8; a single pair of shorter, often mostly fused, "X-shaped" dorsal apophyses located entirely within A8, and an additional short, separated pair located within A8 of *C. aridula*; apex of ovipositor soft, trilobed (one lobe minute), and setose. Ductus bursae highly variable, extremely short and broad in *C. austrina* to long and slender in *C. neblinae*; ductus seminalis usually joined midway along ductus bursae. Corpus bursae moderately enlarged, usually with a single, variably shaped signum; signum absent in *C. aridula*.

Discussion.—A single synapomorphy—the presence of a slender, spinelike process arising from the saccular lobe at the base of the male valva—distinguishes this South American genus from its Old World sistergroup, *Eriocottis*. The type species of *Crepidochares*, however, exhibits several apomorphies that strongly suggest further division within the New World species. Major among these features which sets *C. subtigrina* apart are the loss of ocelli, fasciculate and pedicellate antennal sensilla, reduction of the maxillary palpi to three short segments, and the relatively smooth and porrect labial palpi. Because no synapomorphy is known to link the other four species, all have been retained within *Crepidochares*.

Key to the Species of *Crepidochares*

1. Ocellus absent. Maxillary palpus reduced, three segmented. Labial palpus porrect ..... *C. subtigrina* Meyrick
– Ocellus present. Maxillary palpus five segmented. Labial palpus distinctly upcurved 2
2. Male genitalia with saccular process minute, less than one third the width of valva (Figs. 106, 110). Distribution southern Chile 3
– Male genitalia with saccular spine elongate, more than half the width of valva (Figs. 97, 103). Distribution northern South America 4
3. Forewing with R1 arising from middle of discal cell. Male genitalia (Fig. 84) with subscaphium relatively broad and elongate, arising from gnathos near insertion of valva; valva with a small spinose process arising from saccular lobe free of valva. Female genitalia (Figs. 126, 127) with four pairs of apophyses; signum present ..... *C. austrina* Davis, new species
– Forewing with R1 arising from basal third of discal cell. Male genitalia (Fig. 108) with subscaphium reduced, arising from gnathos above insertion of valva; valva with minute spinose process not projecting beyond margin of valva. Female genitalia (Fig. 130) with five pairs of apophyses; signum absent ..... *C. aridula* Davis, new species
4. Male with length of saccular process equalling width of valva and terminating in a broad truncate spine (Fig. 97); apical half of valva (cucullus) broader than basal half. Female with fourth pair of apophyses within A8 mostly fused and X-shaped (Fig. 121) ..... *C. neblinae*, new species
– Male with length of saccular process less than width of valva and terminating in a slender, minute spine (Fig. 103); apical half of valva

more slender than basal half. Female with fourth pair of apophyses convergent but not fused (Fig. 124) ..... *C. colombiae*, new species

Crepidochares neblinae Davis, New Species

Figs. 1, 16, 17, 22–33, 82, 95–99, 120–122; Map 1

Adult (Fig. 1).—Length of forewing: ♂, 8 mm; ♀, 8.2–8.6 mm. A small moth with grayish forewings marked by three more or less distinct, fuscous cross bands and scattered spots; ocellus present; labial palpus slightly upcurved; male valva with a prominent, blunt tipped, spinose lobe arising from apex of sacculus; female with X-shaped apophyses within eighth abdominal segment.

Head: Vestiture mixed, mostly fuscous near middle bordered by tufts of cream to buff scales laterally and at lower part of frons. Ocellus well developed. Antenna 0.55–0.6 the length of forewing, 39–40 segmented; scape light to medium brown, with a pecten consisting of 8–10 dark brown piliform scales; scales not forming an eyecap; flagellum alternately ringed with dark fuscous and light brown; scales encircling each segment with basal ring fuscous; flagellomeres smooth except for a minute, apical mid-dorsal process (Fig. 23); sensilla relatively short and not fasiculate nor born on tubercules (Figs. 22, 23). Maxillary palpus elongate, 5-segmented; vestiture variable, light to dark brown. Labial palpus slightly upcurved, mostly dark brown to fuscous laterally and pale buff to cream mesally, with apices of second and third segments pale buff; numerous cream to fuscous bristles clustered near apex of second segment.

Thorax: Pronotum light gray strongly irrorated with fuscous tipped scales; tegula mostly brownish fuscous. Venter grayish white to cream. Forewing light gray heavily irorrated with fuscous, most scales with dark fuscous tips; 3 more or less distinct, irregular bands of dark fuscous traversing outer half of wing; subapical band parallel to termen and divergent from medial band; small patches of cream scales scattered mostly along costa and termen and extending out into fringe. Hindwing uniformly gray. Female frenulum consisting of two closely set bristles. Fore- and midlegs gray to dark fuscous dorsally, buff to cream ventrally, generally darker on tibia and tarsus with conspicuous buff apices to each segment and a median ring on tibia. Hindleg much paler, generally gray with tarsomeres darker and indistinctly ringed with cream.

Abdomen: Dark to light gray dorsally, paler ventrally.

Male genitalia: As shown in Figs. 95–99. Uncus lobes reduced. Subscaphium poorly sclerotized, indistinct. Gnathos slender, forming a deep U. Vinculum abruptly constricted to form a moderately elongate, slender saccus. Transtilla relatively broad, lightly sclerotized and highly arched. Valva moderately broad; cucullus rounded; sacculus with a prominent, elongate spinose lobe arising distally; a single, broad, short, truncate spine arising from apex of lobe. Aedoeagus moderately slender, nearly as long as valva, with a small bulbous lobe at base.

Female genitalia: As shown in Figs. 120–122. Four pairs of apophyses present, including moderately long anterior and extremely long posterior pairs, a short ventral pair within A10, and a short dorsal pair within A8 which are fused approximately half their length along middle. Ductus bursae elongate (about equal to length of posterior apophyses), moderately slender, with ductus seminalis joined slightly anterior to middle. Corpus bursae moderately enlarged, with a single, broad, diamond-shaped signum bearing a pair of short, caudally directed spines (Fig. 122).

Holotype.—Female. Camp VII, 1850 m, Cerro de la Neblina, Territorio Federal Amazonas, Venezuela; 2–4 Dec 1984, R. L. Brown (USNM).

Paratypes.—VENEZUELA: Same data as holotype; 2 ♂, 3 ♀, slides USNM 23672, 29987, 30347, 30420. Paratypes deposited in UCVM and USNM.

Host.—Unknown.

Flight period.—December.

Distribution (Map 1).—Known only from one collecting site on Cerro de la Neblina, Venezuela, which is situated near the Brazilian border at 1850 meters and 0°51′N, 6°58′W.

Etymology.—The specific epithet is derived from the name of the general type locality, Cerro de la Neblina (Mountain of the Mist).

Discussion.—Both male and female genital morphology easily distinguishes this species. The spinose lobe of the male valva is the largest of the five currently recognized species of *Crepidochares*, with an apical spine which is not only the largest, but also the only one that is truncate.

Rather intensive collecting during the Cerro de la Neblina expeditions at the Amazonian basecamp site (130 m), did not reveal the presence of this species at lower elevations. Collections on the rather large and topographically diverse massif of Neblina itself were relatively sparse and undoubtedly inadequate for Lepidoptera. Only the earliest (December) collections at camp VII (1850 m) resulted in specimens of *C. neblinae*. All were attracted to ultraviolet lights.

Crepidochares colombiae Davis, New Species

Figs. 2, 100–103, 123–125; Map 1

Adult (Fig. 2).—Length of forewing: ♂, 9–9.5 mm; ♀, 11 mm. A small moth with light brown forewings heavily mottled with dark brown striae and bands; ocellus present; labial palpus slightly upcurved; male valva with long slender spinose lobe arising from apex of sacculus; female with fourth pair of dorsal apophyses converging caudally but not fused.

Head: Vestiture mostly brown, slightly paler and more buff near occiput. Ocellus well developed. Antenna 0.4–0.5 the length of forewing, 40 segmented; scape with 8–10 dark brown piliform scales forming distinct pecten; scales not forming an eyecap; scape and flagellum with dorsal half uniformly covered with dark brown scales, ventral half naked except for dense pubescence of sensilla. Maxillary palpus elongate, 5-segmented; vestiture light brown dorsally, dull white ventrally. Labial palpus uniformly brown laterally, dull white to pale buff mesally; dorsal apex of second segment with a tuft of brown bristles, a few scattered bristles also along dorsal margin; ventral margin rough, with numerous bristles.

Thorax: Pronotum uniformly dark brown. Venter white to pale buff. Forewing pale buff, heavily mottled with dark brown; three dark brown bands usually distinct across distal ⅔ of wing; basal two bands strongly oblique and parallel; distal band parallel to termen; all 3 bands sometimes coalescing to form a "W" shaped patten; a fine reticulate network of dark brown lines and spots scattered between bands and along costal margin; termen mostly dark brown interrupted with 3–4 light brown to buff spots. Hindwing uniformly dark gray. Female frenulum consisting of four bristles. Foreleg dark brown dorsally, light brown ventrally with apices of tarsal and tibial segments and middle of tibia ringed with buff. Midleg similarly marked but generally paler. Hindleg very pale, uniformly pale buff except for slight brownish banding on tarsomeres.

Abdomen: Dark brown dorsally, buff ventrally.

Male genitalia: As shown in Figs. 100–103. Uncus lobes slender, acute, and widely spaced. Subscaphium poorly sclerotized, indistinct. Gnathos indistinct, membranous. Vinculum constricted to form a short, slender saccus. Transtilla a slender arch between bases of valvae. Valva moderately broad, gradually narrowing to apex; an elongate, spi-

nose process arising from apex of sacculus; apex of process with a slender spine. Aedoeagus moderately slender, slightly curved, especially at base, and approximately ⅔ the length of valva.

Female genitalia: As shown in Figs. 123–125. Four pairs of apophyses present, including moderately long anterior and extremely long posterior pairs, a short ventral pair within A10, and a short dorsal pair within A8 which converge at their caudal ends but do not fuse. Ductus bursae moderately long, approximately half the length of posterior appophyses, with ductus seminalis joined at middle. Corpus bursae greatly enlarged, with a single, highly irregular, transverse signum (Fig. 125).

Holotype.—Male. Sierra del Libano, 6000 ft. [1829 m], Colombia; May 1899, H. H. Smith, 68622, slide 19243 (BMNH).

Paratypes.—COLOMBIA: Same locality as holotype, 10 ♂, 1 ♀, nos. 68613–21, 68623–24, 68720–21; slides BMNH 19247, USNM 30423. Paratypes deposited in BMNH and USNM.

Host.—Unknown.

Flight period.—May.

Distribution (Map 1).—Known only from the type locality, Sierra del Libano, also known as El Libano, which according to Paynter and Traylor (1981) is a dense subtropical forest and a spur of the Cuchilla San Lorenzo on the southwestern Sierra Nevada de Santa Marta in Magdalena Province (ca. 11°10′N, 74°W).

Etymology.—The specific name is derived from the country of origin, Colombia.

Discussion.—This species is the largest and darkest in color within the genus. It is also the only species of *Crepidochares* (of which females are known) in which the dorsal apophyses (fourth pair) of the eighth abdominal segment do not fuse but remain separate, although strongly convergent. *Crepidochares colombiae* appears most allied to *C. neblinae* on the basis of general morphology, particularly the well developed saccular process of the male.

Crepidochares austrina Davis, New Species

Figs. 3, 84, 104–107, 126–128; Map 2

Adult (Fig. 3).—Length of forewing: ♂, 4.6–6 mm; ♀, 5.8–6.1 mm. A small moth with buff to light brown forewings variably marked with reddish brown to dark fuscous spots and costal strigulae; male valva with a small spinose process arising from saccular lobe; female ovipositor with four pairs of apophyses.

Head: Vestiture pale grayish white to buff with a slight concentration of more brownish scales across upper frons between antennal bases. Antenna 0.6–0.7 the length of forewing, approximately 38 segmented; scape fuscous at base, pale buff apically; scales not forming an eyecap; pecten with 6–8 long light brown piliform scales; flagellum with ventral half naked and densely ciliate, dorsal half covered with alternating bands of pale buff and fuscous scales. Maxillary palpus pale buff. Labial palpus pale buff, lightly irrorated with fuscous on second segment, more heavily so on third; apex and outer side of second segment with 4–6 long, fuscous, bristlelike scales.

Thorax: Pronotum light bronzy brown, irrorated with darker and paler brownish scales. Forewing of similar color with a complex pattern of pale buff to reddish brown and dark fuscous scales; distal half of costa with an alternating pattern of about six buff strigulae interspersed by fuscous; oblique fuscous banding slightly evident but obscure due to rubbed condition of specimens. Hindwings uniformly shiny gray with an elongate fringe about ¾ the width of wing. Venter of thorax uniformly dull white to pale buff. Legs generally dark grayish fuscous dosally and whitish to buff ventrally, gradually becoming almost entirely whitish to buff on hindleg; tibia and tarsus of fore and midleg with grayish to fuscous banding.

Abdomen: Shiny grayish fuscous dorsally, pale buff ventrally.

Male genitalia: As shown in Figs. 104–

107. Uncus lobes moderately long and stout. Subscaphium relatively elongate and broad, approximately 0.5 the width of genital capsule, joined to arms of gnathos near insertion of valvae. Vinculum tapering gradually anteriorly, V-shaped. Valva with ventral margin deeply emarginate near middle, abruptly marking end of sacculus; a small spinose process arising from inner angle of saccular lobe; ventral margin along more narrow, distal half with 5–6 large spinose setae; basal apophysis of valva broadly triangular. Aedoeagus without cornuti, approximately ¾ the length of valva.

Female genitalia: As shown in Figs. 126–128. Four pairs of apophyses present with only a single, dorsal pair in A8, approximately 65% fused. Ductus bursae short, broad, barely perceptible from moderately enlarged corpus bursae; signum consisting of a single cluster of minute, stout spines (Fig. 128).

Holotype.—Female. Anticura, 350 m, Parque Nacional Puyehue, Osorno Prov., Chile; 18 Nov. 1981, Nielsen and Karsholt (ZMHU).

Paratypes.—CHILE: Maule Prov: Paso Garcia, 300 m, ca. 23 km NW Cauquenes: 1 ♂, 29–30 Nov. 1981, D. R. Davis, slide USNM 29581. Rio Teno, 800 m, ca. 40 km E. Curico: 1 ♂, 25–27 Nov. 1981, D. R. Davis, slide USNM 29583. Ñuble Prov: Alto Tregualemu, 500 m, ca. 20 km SE Chovellen: 1 ♂, 1–3 Dec. 1981, D. R. Davis, slide USNM 29580. Osorno Prov: Same data as holotype, 1 ♂, slide DRD 3708; 1 ♂, 17 Dec. 1981, Nielsen and Karsholt. Valdivia Prov: Rincon de la Piedra, 180 m, 20 km S. Valdivia: 1 ♂, 5 ♀, 15 Nov. 1981, Nielsen and Karsholt, slides USNM 23599, 29504. Paratypes deposited in ANIC, BMNH, USNM, and ZMHU.

Host.—Unknown.

Flight period.—November 15 to December 17, univoltine.

Distribution.—This species occurs further south than does *aridula*, and is found within the principal range of *Nothofagus*. It has been found as far north as the Rio Teno, which approximately marks the northern limits of the Northern Valdivian Forest zone, and extends as far south as Valdivia and Osorno Provinces, which are located well within the more southern Valdivian Forest zone.

Etymology.—The specific name is derived from the latin *austrinus* (southern) as suggested by its more southern distribution when compared to the only other Chilean eriocottid, *aridula*.

Discussion.—*Crepidochares austrina* is easily distinguished from the other members of *Crepidochares* by major differences in venation and both male and female genitalia, as summarized in the key to species. The first radial vein in the forewing is characteristic in arising more distad from the middle of the discal cell. In contrast to *C. aridula*, the ovipositor of *C. austrina* possesses the normal (for Eriocottidae) four pairs of apophyses, including a short, mostly fused dorsal pair in A8. Present distributional data suggest that it may also be more adapted to the wetter Valdivian forests of southern Chile.

Crepidochares aridula Davis, New Species

Figs. 4, 5, 18, 19, 34–57, 85–90, 108–112, 129, 130; Map 2

Adult (Figs. 4, 5).—Length of forewing: ♂, 5.2–6.1 mm; ♀, 4.5 mm. A small moth with light gray forewings variably marked with reddish brown to fuscous spots and oblique bands; male valva relatively simple, with a minute spinose lobe from distal end of sacculus; female ovipositor with five pairs of apophyses.

Head: Vestiture pale grayish white to buff with a small lateral tuft of darker scales arising immediately posterior to ocellus and another near front rim of eye. Antenna 0.65 the length of forewing, approximately 31 segmented; scape pale gray irrorated with brown; scales not forming an eyecap; pecten with 6–8 long brownish piliform scales; fla-

gellum with ventral half naked and densely ciliate, dorsal half covered with alternating bands of grayish white and fuscous scales. Maxillary palpus grayish white to buff. Labial palpus light brown over basal segments; apical segment mostly covered with divergent, pale whitish buff scales; a few bristle-like brown scales arising from apex of second segment.

Thorax: Pronotum pale buff to grayish white, irrorated with darker reddish brown to fuscous scales. Forewing of similar color with a distinct pattern of oblique bands (Figs. 1–2) evident on fresh specimens. Hindwing uniformly pale gray with elongate fringe nearly equalling width of hindwing. Venter of thorax grayish white. Legs mostly dull white ventrally, brown dorsally with two broad fuscous bands usually evident on tibia; base of all tarsal segments dark fuscous.

Abdomen: Uniformly shiny pale buff to grayish white.

Male genitalia: As shown in Figs. 108–112. Uncus lobes slender, short. Subscaphium moderately slender and short, joined to arms of gnathos well above insertion of valvae. Vinculum narrowing abruptly anteriorly to form a moderately broad saccus. Valva relatively simple, ventral margin with saccular lobe slightly developed and bearing a single minute spinose lobe; basal saccular area approximately twice the width of distal half; basal apophysis of valva elongate and slender. Aedoeagus simple, without cornuti, approximately equalling valva in length.

Female genitalia: As shown in Figs. 129, 130. Five pairs of apophyses present, including elongate anterior and posterior apophyses, a short ventral pair within A10, and two pairs of dorsal apophyses within A8, one pair of which are fused about 70% their length. Ductus bursae extremely slender. Corpus bursae moderately enlarged, without signum.

Holotype.—Male. Rio Colorado, ca. 40 km SE Santiago, 1100 m, Metropolitan Region, Chile; 29–31 Oct. 1981, Don and Mignon Davis, USNM.

Paratypes.—CHILE: Same data as holotype; 7 ♂, slides USNM 29503, 29587, 22140. Curico Prov. Potrero Grande, 35 km SE Curico, 35°12.5'S, 71°W; 1 ♂, 6 Dec. 1982, R. L. Brown, USNM slide 29584. 10 km NW Rauco, 34°52'S, 71°21'W; 1 ♀, 2 Dec. 1982, USNM slide 29582. Paratypes deposited in ANIC, MHNS, and USNM.

Host.–Unknown.

Flight period.—October 29 to December 6; univoltine.

Distribution.—Known only from the Central Valley Biotic Province and lower elevations of the adjacent Central Andean Cordillera Province of central Chile. The forests of these areas are relatively dry and are situated just north of the principal northern limits of *Nothofagus*.

Etymology.—The specific name is derived from the Latin *aridulus* (diminutive of dry) in reference to the more xeric habitat of this species.

Discussion.—*Crepidochares aridula* differs considerably from the only other Chilean eriocottid, *C. austrina*, by major differences in venation and the genitalia of both sexes, as summarized in the key to species. The forewing venation of *C. aridula* agrees more with the other species of *Crepidochares* and *Eriocottis* in possessing a more basal origin for R1. Of the five recognized species of New World Eriocottidae, the male valva of *C. aridula* has the most reduced saccular spine. The female ovipositor is unique among Lepidoptera by the presence of five pairs of apophyses. The extra fifth set is believed to be derived from the caudal ends of the anterior apophyses. In addition, *C. aridula* exhibits a generally paler color than *C. austrina*. Its range may also be confined to the drier, more northern non-*Nothofagus* forests of central Chile. All specimens were collected in UV light traps.

Because the sole female specimen of this species has not been collected in close association with any males and is slightly smaller in size with more distinctly marked forewings, its identity remains somewhat in

doubt. Association of males and females needs confirmation in particular because the most unusual apomorphy (i.e. the fifth pair of apophyses) of the species occurs only in the female.

Crepidochares subtigrina Meyrick
Figs. 6, 58–63, 83, 113, 114; Map 1

Crepidochares subtigrina Meyrick, 1922: 601.—Fletcher, 1929: 58.—Clarke, 1955: 298; 1970: 36.—Davis, 1984: 21.

Adult (Fig. 6).—Length of forewing: ♂, 7.8 mm. A small moth with pale yellowish forewings irregularly marked with slightly darker, more brownish transverse bands and spots; ocellus absent; labial palpus porrect; male valva with a stout spinose lobe arising from apex of sacculus; female unknown.

Head: Vestiture pale cream to white. Ocellus absent. Antenna 0.7–0.8 the length of forewing, approximately 40 segmented; scape pale cream, with approximately 12 piliform cream colored scales forming a pecten; scales dorsad to pecten extending forward to form a broad eyecap; flagellum dorsally covered with pale cream scales; ventrally the flagellum is strongly ciliate with most sensilla clustered on two pairs of short pedicels (Figs. 58–60), with apical pair arising more approximate. Maxillary palpus greatly reduced, 3-segmented with apical segment slightly larger, covered with a few pale cream scales. Labial palpus pale buff to cream, irrorated with slightly darker tipped scales; vestiture broad near base, gradually tapering to apex; strongly porrect, completely smooth and without bristles.

Thorax: Pronotum cream, slightly darker and more brown over tegula. Venter cream. Forewing cream to pale yellow crossed by several, slightly darker yellow brown bands or strigulae, basal three slightly darker and most distinct; subapical two bands very indistinct and interrupted; apical band very pale but entire; fringe cream. Hindwing uniformly pale cream. Foreleg cream with darker brown suffusion dorsally over tibia and tarsus; hindleg uniformly pale cream.

Abdomen: Color not examined (on slide).

Male genitalia: As shown in Figs. 113, 114. Uncus lobes moderately long and stout. Subscaphium poorly sclerotized, indistinct. Gnathos slender, forming a deep V. Vinculum tapering anteriorly, with a slight constriction near base. Transtilla slender. Valva slender, with 3–4 stout, spinose setae arising near middle immediately distad to spinose lobe from sacculus. Aedoeagus moderately stout, approximately 0.6 the length of genital capsule, without cornuti.

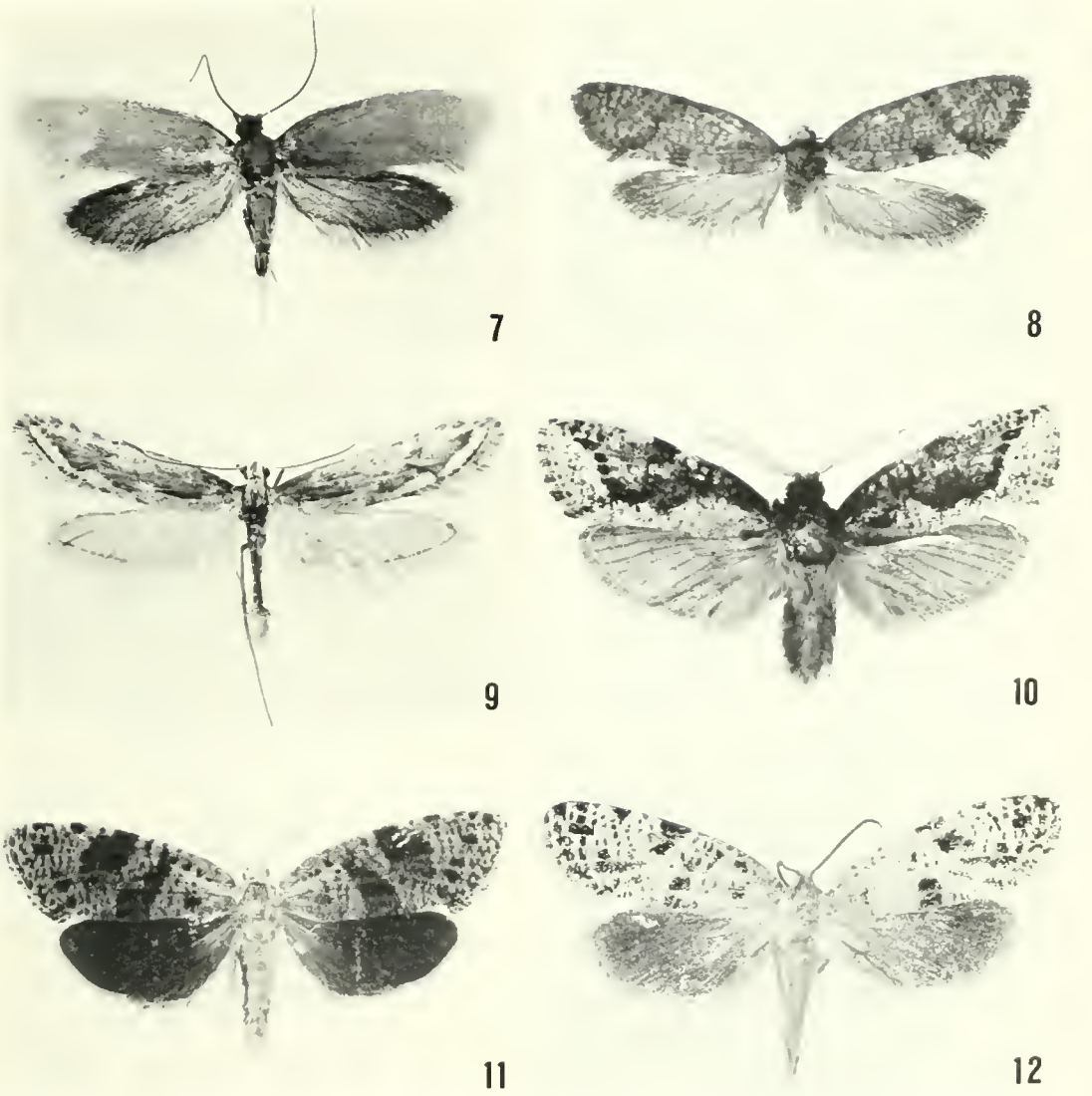
Type.—Holotype. ♂; BMNH.

Distribution (Map 1).—Known only from the holotype, which was collected in October by Parish along the Amazon River at Parintins, Amazonas, Brazil.

Discussion.—Since its discovery, *Crepidochares subtigrina* has been consistently regarded as a member of the Tineidae. As stated in the key to species and elsewhere, numerous apomorphies distinguish this species, still represented by only the male holotype. The male genitalia, especially the prominent spinose process arising from the sacculus, clearly associates *C. subtigrina* with the other members of the genus. Although Meyrick describes the ocelli as "posterior," no ocelli were observed on the holotype.

In addition to its rather aberrant morphology, *C. subtigrina* is of further interest in being the only South American eriocottid discovered thus far from the lowland tropics. The other four species described herein are either from montane or southern temperate habitats.

Figs. 1–6. Adult Eriocottidae. 1, *Crepidochares neblinae* n. sp., female holotype, Venezuela (8.5 mm). 2, *Crepidochares colombiae* n. sp., male holotype, Colombia (9 mm). 3, *Crepidochares austrina* n. sp., male holotype, Chile (6 mm). 4, *Crepidochares aridula* n. sp., male holotype, Chile (5.8 mm). 5, *Crepidochares aridula* n. sp., female paratype, Chile (4.7 mm). 6, *Crepidochares subtigrina* Meyrick, male holotype, Brazil (7.8 mm). (Length of forewing in parentheses.)



Figs. 7–12. Adult Eriocottidae. 7, *Eriocottis fuscanella* Zeller, male [Europe] (8 mm). 8, *Eriocottis flavicephalana* Issiki, male holotype, Taiwan (8.5 mm). 9, *Deuterotinea casanella* (Eversmann), male [Europe] (10.2 mm). 10, *Compsoctena thwaitesi* (Walsingham), male, Sri Lanka (15.5 mm). 11, *Compsoctena aethalea* (Meyrick), male, India (14.8 mm). 12, *Compsoctena aethalea* (Meyrick), female, India (18 mm). (Length of forewing in parentheses.)

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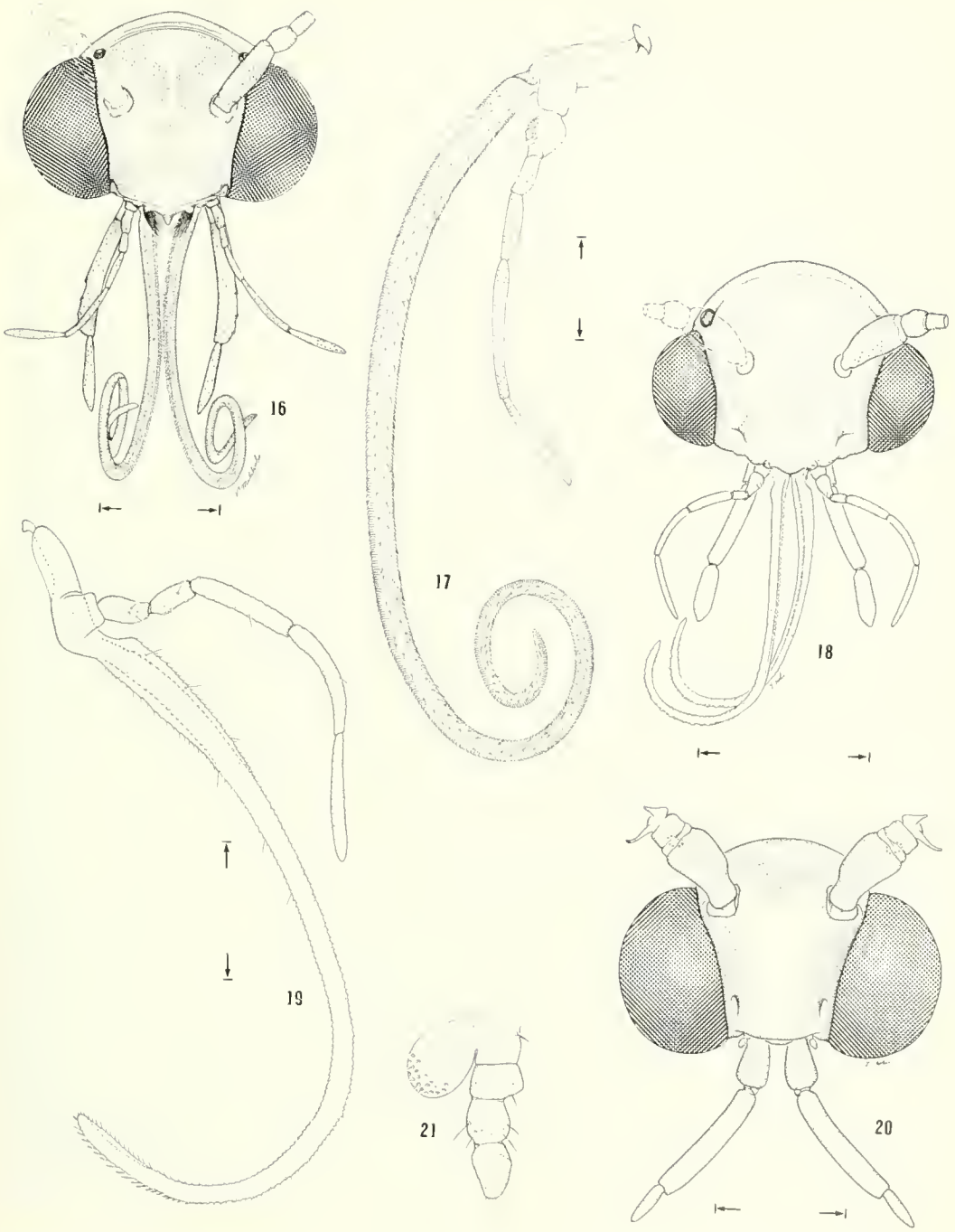
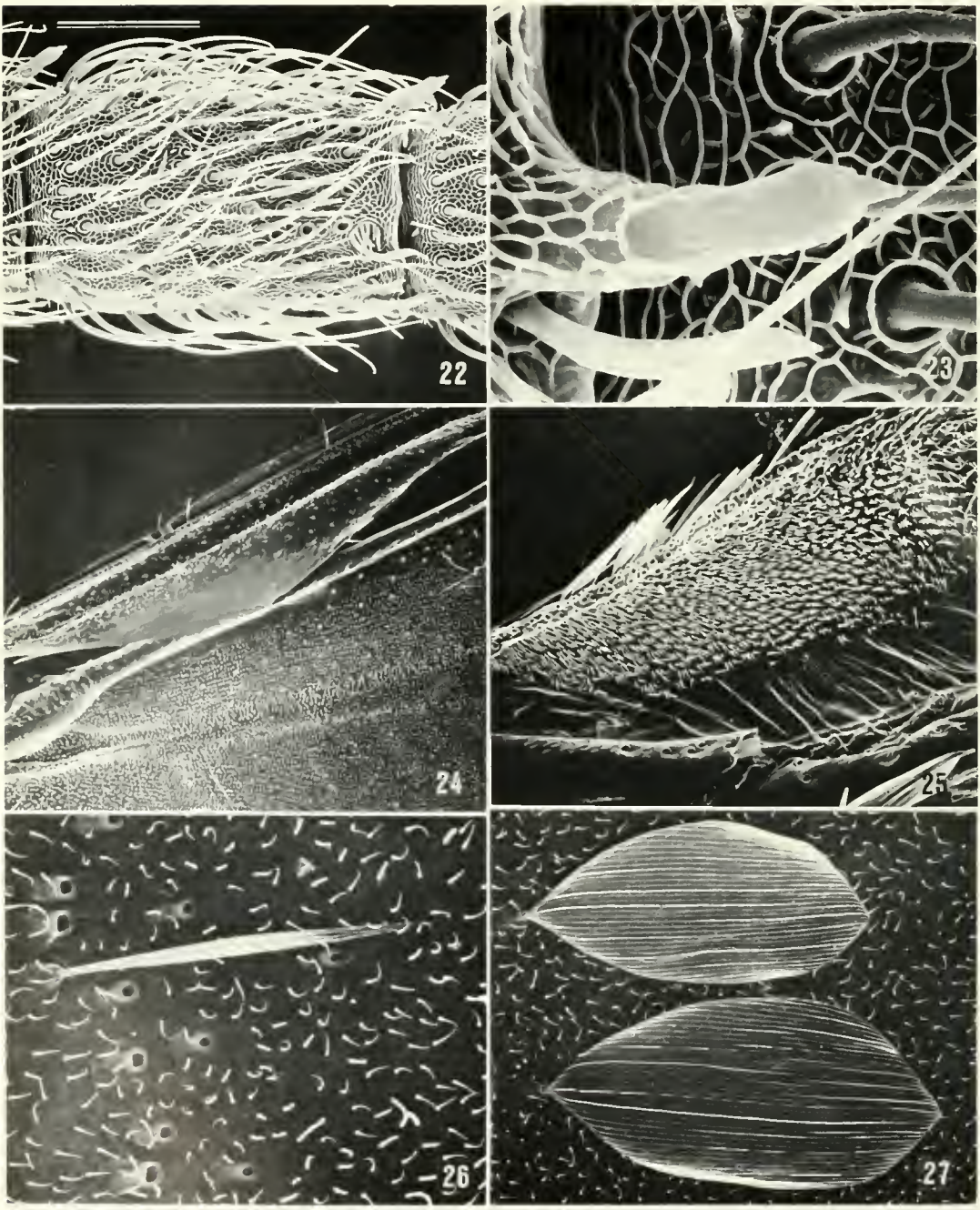
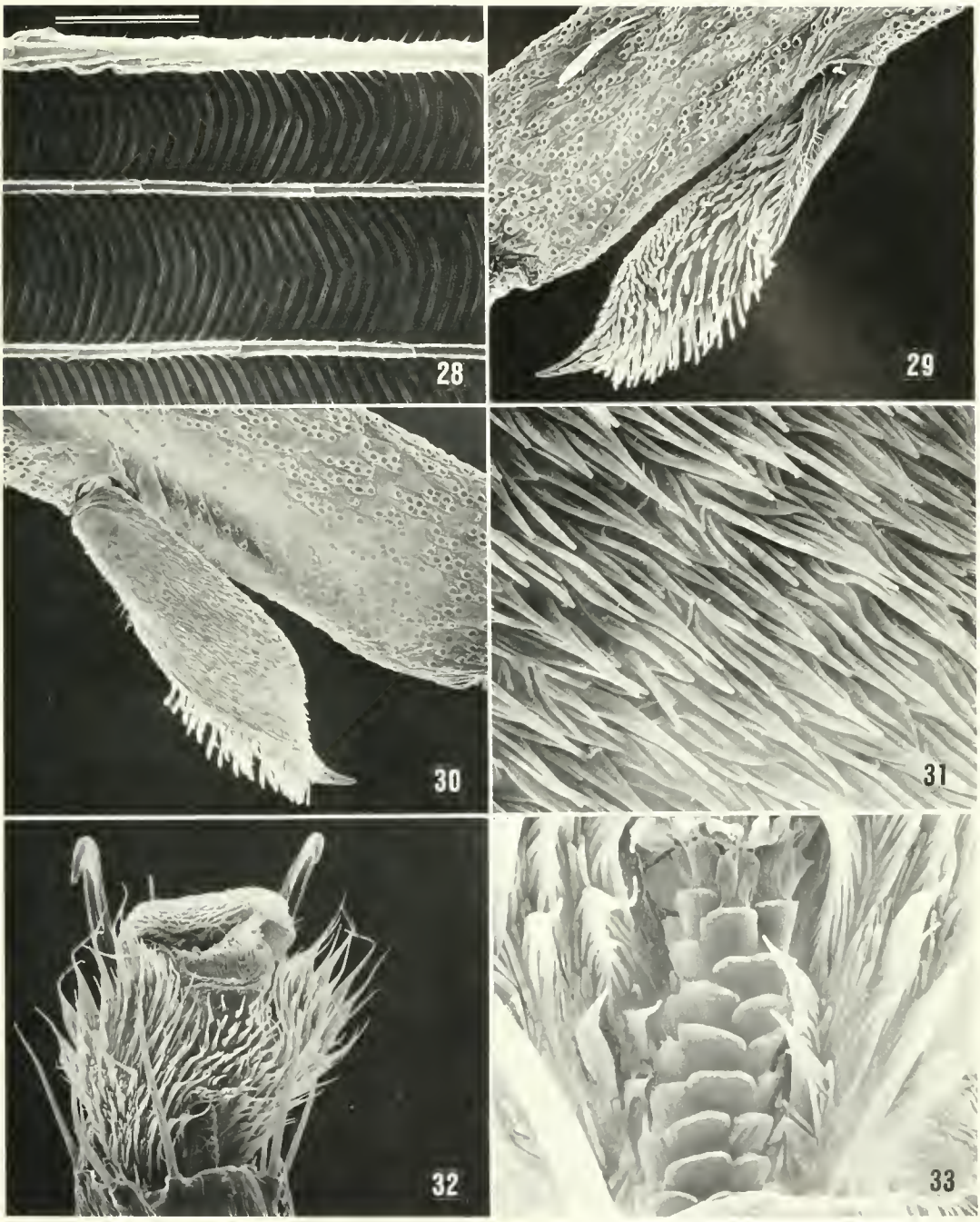
Figs. 13–15. Lateral view of heads. 13, *Crepidochares colombiae* n. sp. 14, *Crepidochares subtigrina* Meyrick, right side, antenna removed. 15, Left side of Fig. 14, note antennal "eyecap."



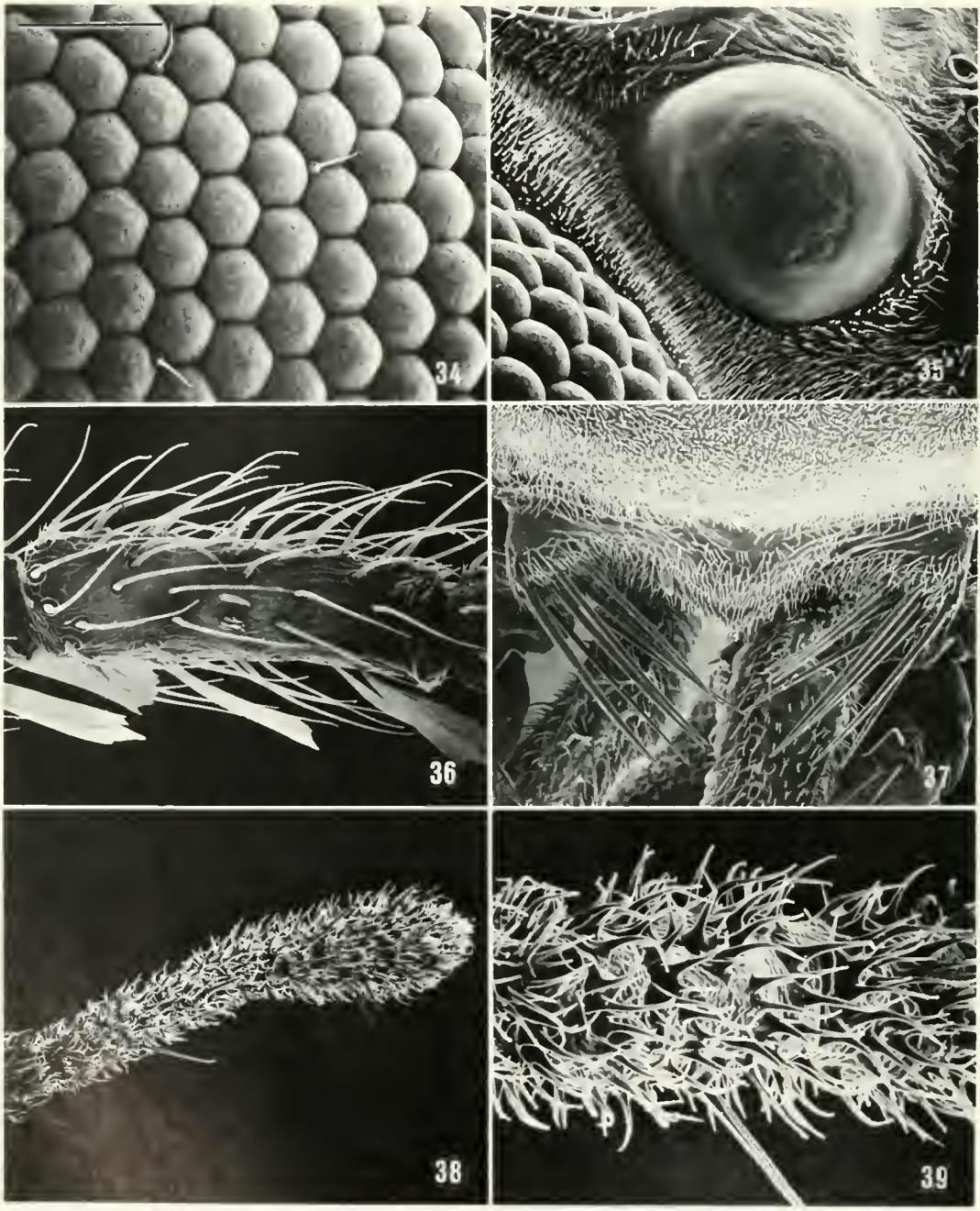
Figs. 16–21. Head structure. 16, *Crepidochares neblinae* n. sp., anterior view (0.5 mm). 17, Maxilla of Fig. 16 (0.2 mm). 18, *Crepidochares aridula* n. sp., anterior view (0.5 mm). 19, Maxilla of Fig. 18 (0.2 mm). 20, *Compsoctena thwaitesii* (Walsingham), anterior view (0.5 mm). 21, Maxilla of Fig. 20 (0.2 mm). (Scale lengths in parentheses.)



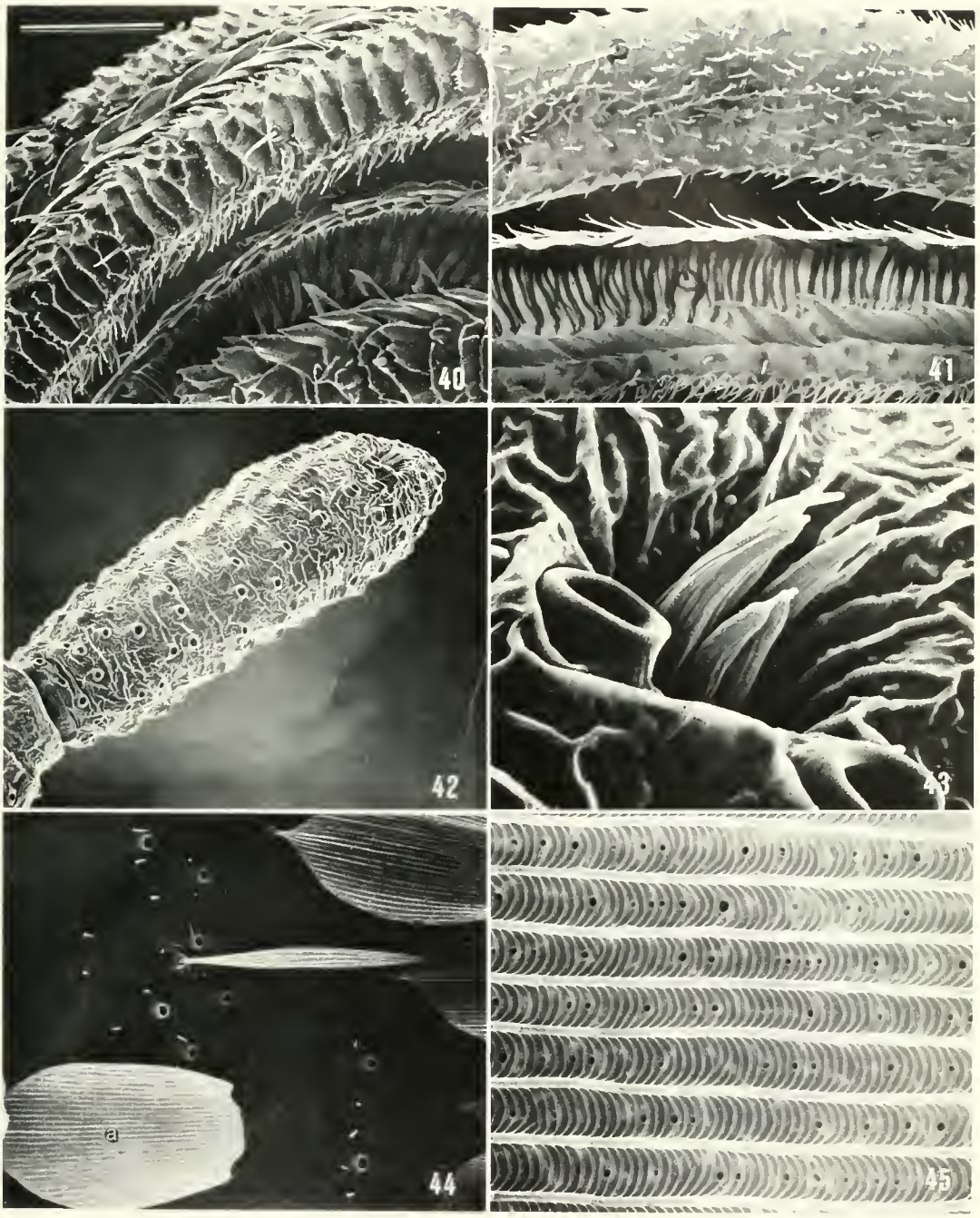
Figs. 22–27. *Crepidochares neblinae* n. sp. 22, Tenth antennal segment, lateral view (43 μm). 23, Mid dorsal antennal process, dorsal view of Fig. 22 (7.5 μm). 24, Subcostal retinaculum, male, ventral forewing (0.3 mm). 25, Subhumeral microtrichia zone, ventral forewing (86 mm). 26, Microtrichia of dorsal forewing, subcostal area (30 μm). 27, Dorsal hindwing, basal half (60 μm); note scale ridge dimorphism. (Scale lengths in parentheses; bar scale for all photographs = Fig. 22.)



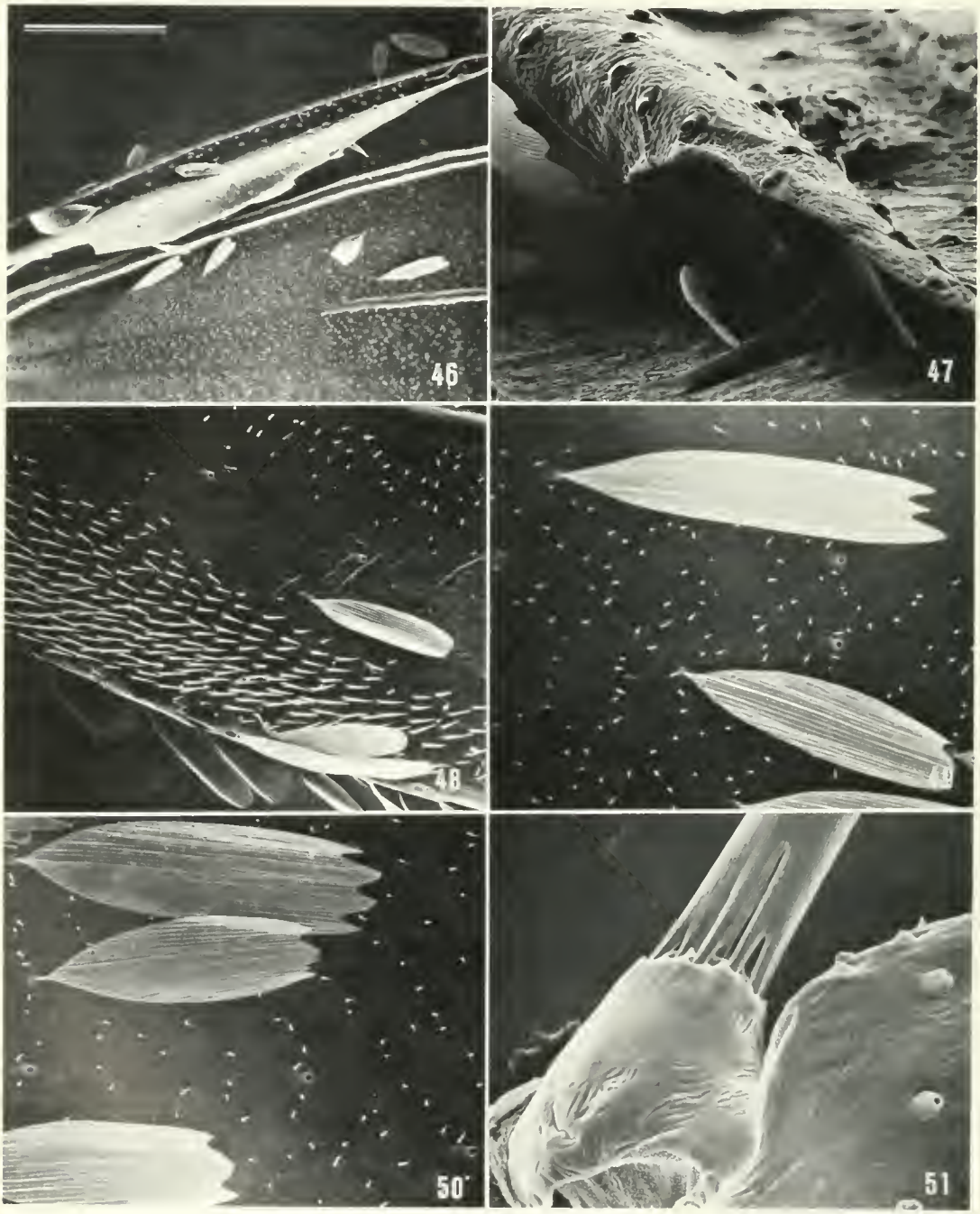
Figs. 28–33. *Crepidochares neblinae* n. sp. 28, Scale structure of "a" in Fig. 27 (2 μm). 29, Inner (ventral) view of epiphysis (75 μm). 30, Outer (dorsal) view of epiphysis (75 μm). 31, Surface detail of Fig. 30 (7.5 μm). 32, Pretarsus of foreleg, ventral view (30 μm). 33, Detail of unguitractor plate in Fig. 32 (7.5 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 28.)



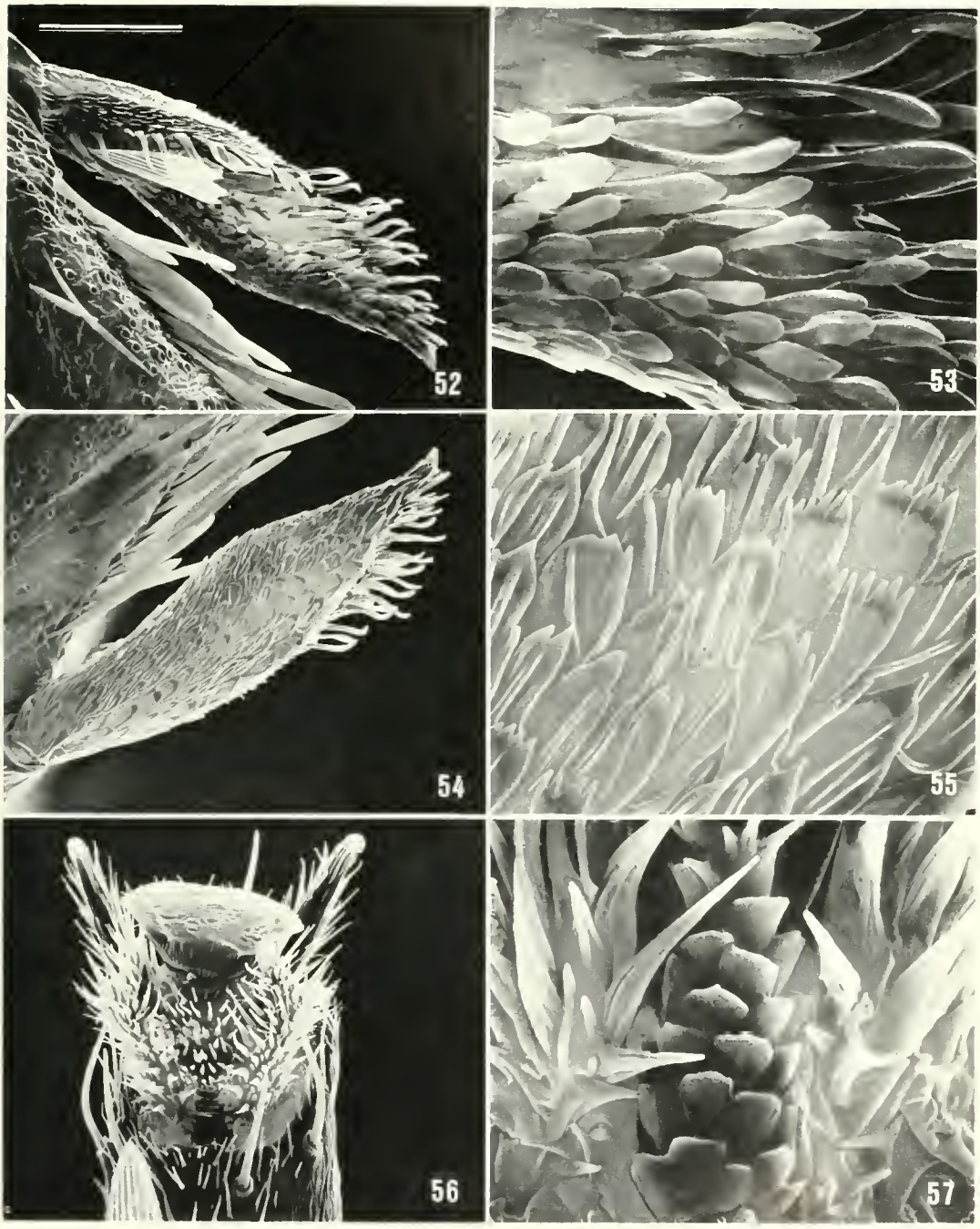
Figs. 34–39. *Crepidochares aridula* n. sp., head structure. 34, Interfacetal setae of compound eye (30 μm). 35, Ocellus (30 μm). 36, Flagellar segment with numerous sensilla trichodea and two sensilla coeloconica (38 μm). 37, Labrum with pilifers (50 μm). 38, Apical (fifth) segment of maxillary palpus (43 μm). 39, Detail of Fig. 38 showing dense cuticular spines (12 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 34.)



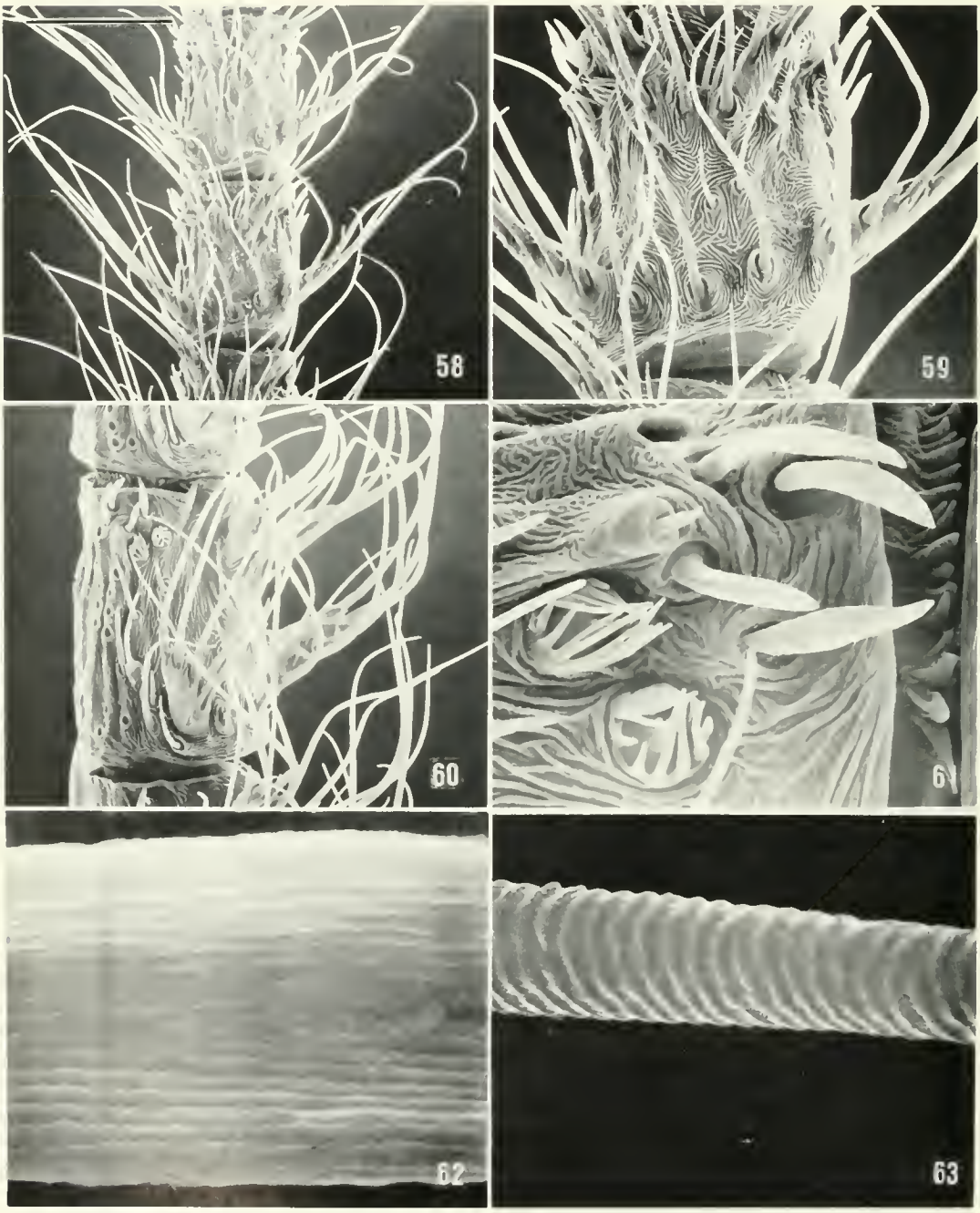
Figs. 40–45. *Crepidochares aridula* n. sp., head and scale structure. 40, Haustellum near base showing imbricate plates (30 μm). 41, Haustellum near middle (and distad) showing external cuticle and food canal (30 μm). 42, Apical (third) segment of labial palpus with subapical sensory pit (50 μm). 43, Detail of sensilla in labial sensory pit (5 μm). 44, Wing scales and microtrichia, discal cell area of dorsal forewing (38 μm). 45, Scale structure of "a" in Fig. 44 (3 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 40.)



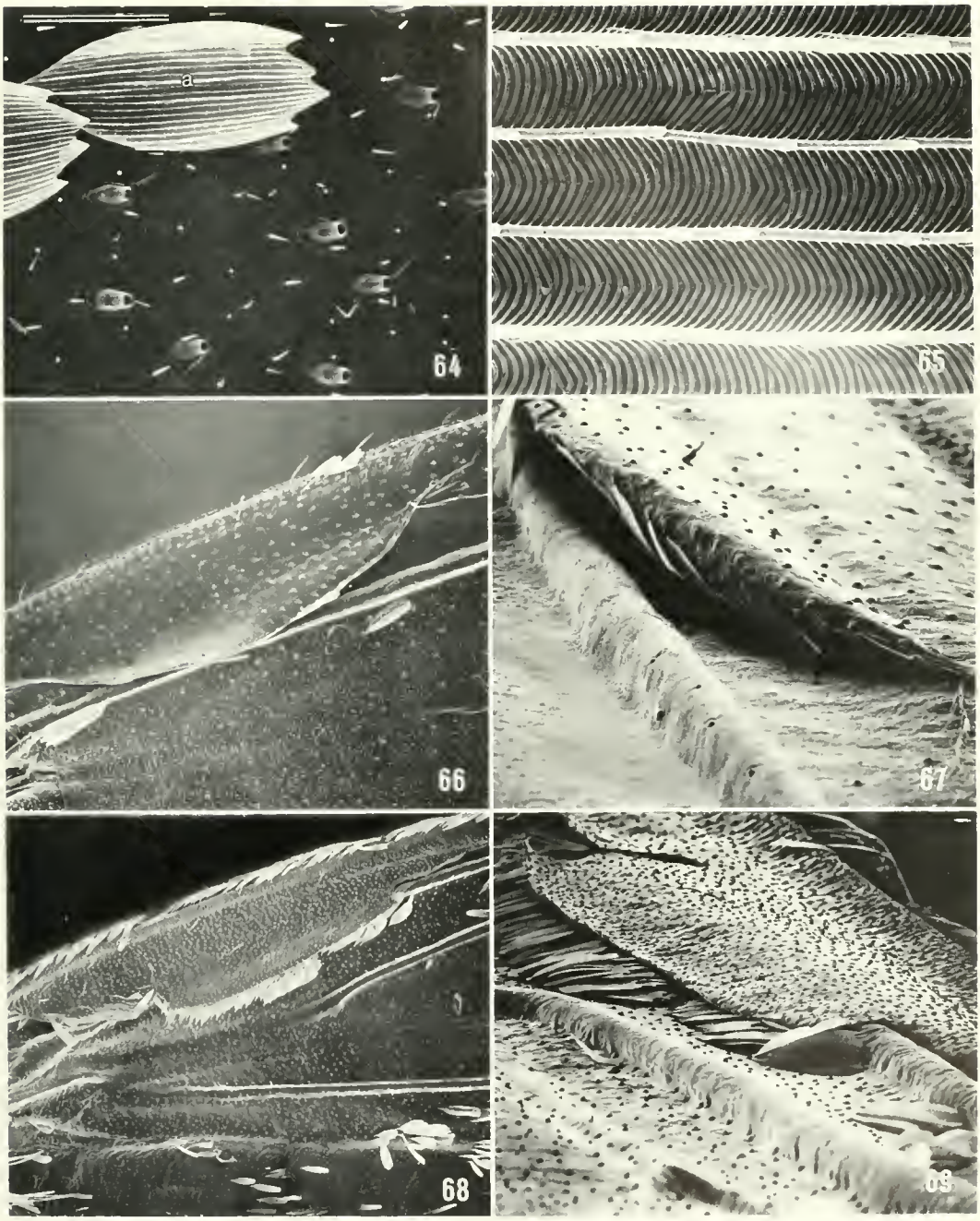
Figs. 46–51. *Crepidochares aridula* n. sp., wing structure. 46, Subcostal retinaculum, male, ventral forewing (231 μm). 47, Distal view of male retinaculum (Fig. 46) (30 μm). 48, Anal margin of ventral forewing showing interlocking microtrichia and general wing microtrichia (75 μm). 49, Wing scales and microtrichia of discal cell area of ventral forewing (50 μm). 50, Scales and microtrichia near apex of discal cell of dorsal hindwing (50 μm). 51, Base of male frenulum (38 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 46.)



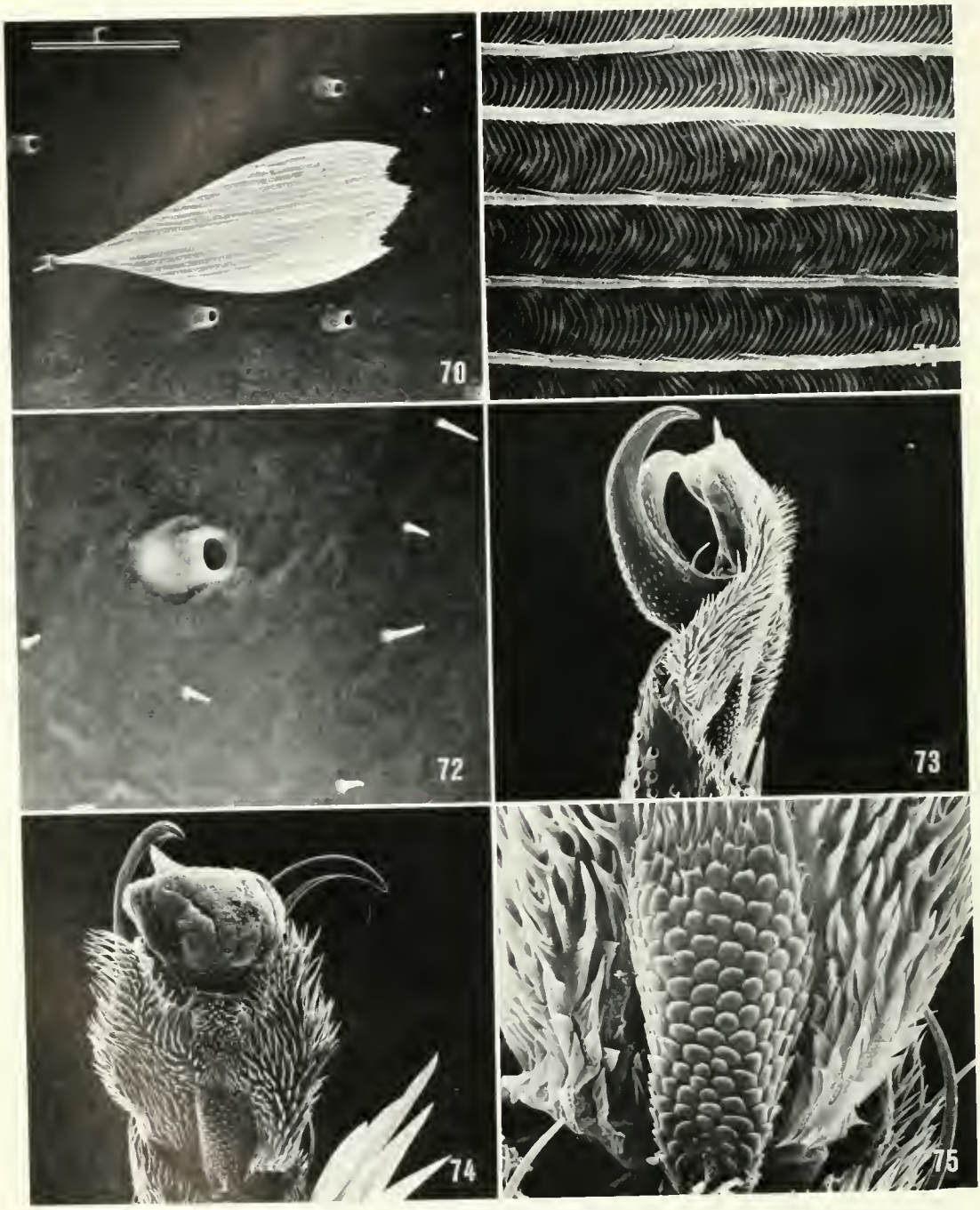
Figs. 52–57. *Crepidochares aridula* n. sp., male leg structure. 52, Epiphysis, posterior view (50 μm). 53, Detail of Fig. 52 showing cleaning spines (i.e., pecten) (12 μm). 54, Epiphysis, anterior view (50 μm). 55, Detail of imbricated spines of Fig. 54 (10 μm). 56, Foreleg pretarsus, ventral view (23.1 μm). 57, Detail of pretarsal unguitractor plate of foreleg (5 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 52.)



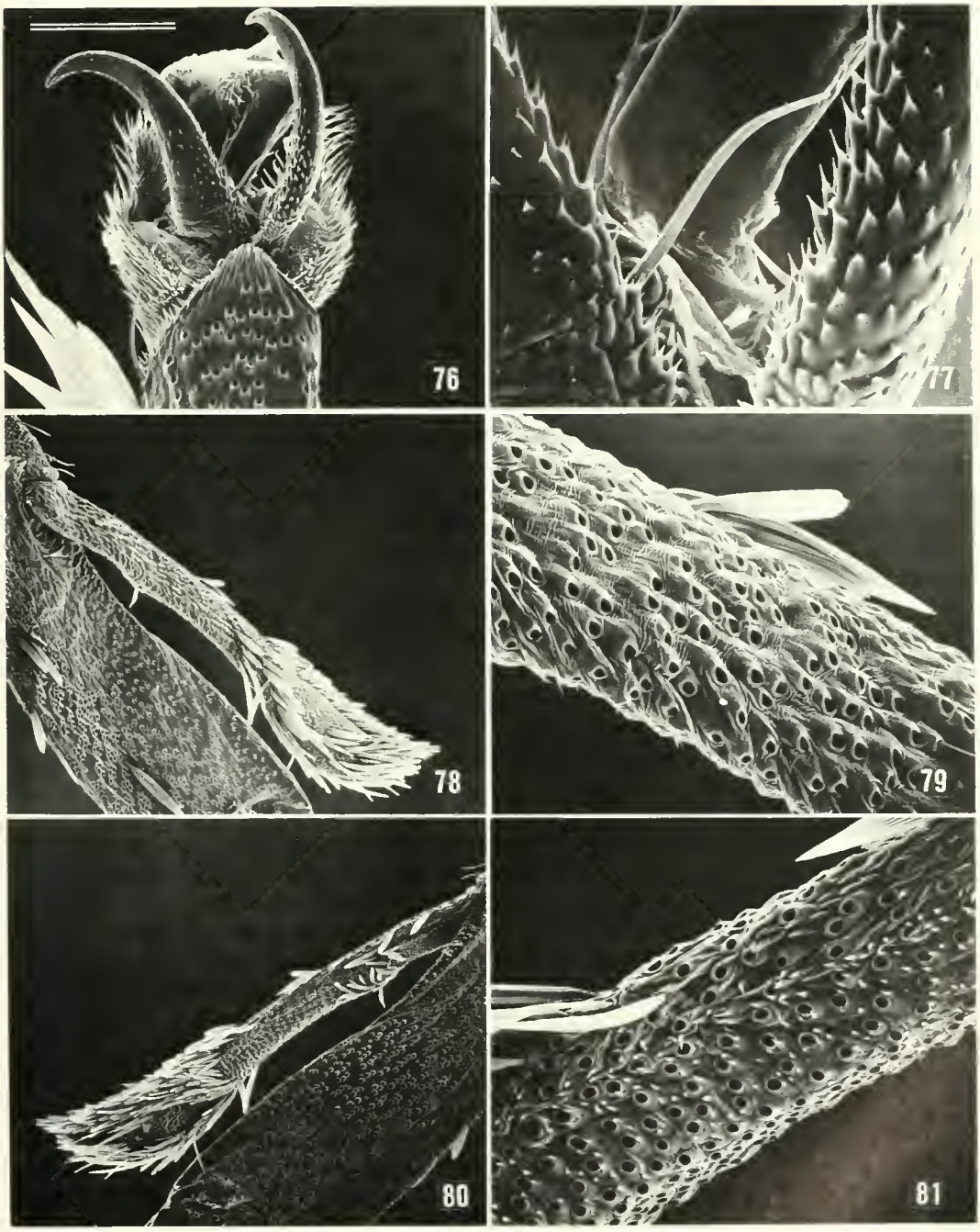
Figs. 58–63. *Crepidochares subtigrina* Meyrick, antennal structure. 58, Segments 7–8, ventral view (86 μm). 59, Detail of seventh segment, Fig. 58 (38 μm). 60, Lateral view of seventh segment (50 μm). 61, Detail of sensilla trichodea and coeloconica in Fig. 60 (10 μm). 62, Surface detail of sensilla trichodea (a) in Fig. 61 (1 μm). 63, Detail of elongate sensilla chaetica from ventral tubercle, seventh segment (1.5 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 58.)



Figs. 64–69. *Eriocottidae*, wing structure. 64, *Eriocottis fuscanella* Zeller, wing scales and microtrichia on ventral forewing near middle of discal cell (43 μm). 65, Detail of scale "a" in Fig. 64 (3 μm). 66, Subcostal retinaculum of male, ventral forewing (0.3 mm). 67, Distal-lateral view of retinaculum (Fig. 66) (75 μm). 68, *Compsoctena thwaitesii* (Walsingham), subcostal retinaculum of male (1.0 mm). 69, Distal-lateral view of retinaculum (Fig. 68) (0.27 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 64.)



Figs. 70–75. *Compsoctena thwaitesii* (Walsingham), male wing and leg structure. 70, Wing scale and microtrichia near dorsal apex of forewing (50 μm). 71, Detail of scale in Fig. 70 (3.8 μm). 72, Detail of microtrichia in Fig. 70 (20 μm). 73, Foreleg pretarsus, lateral view (100 μm). 74, Foreleg pretarsus, ventral view (100 μm). 75, Hindleg pretarsus, detail of unguitractor plate (30 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 70.)



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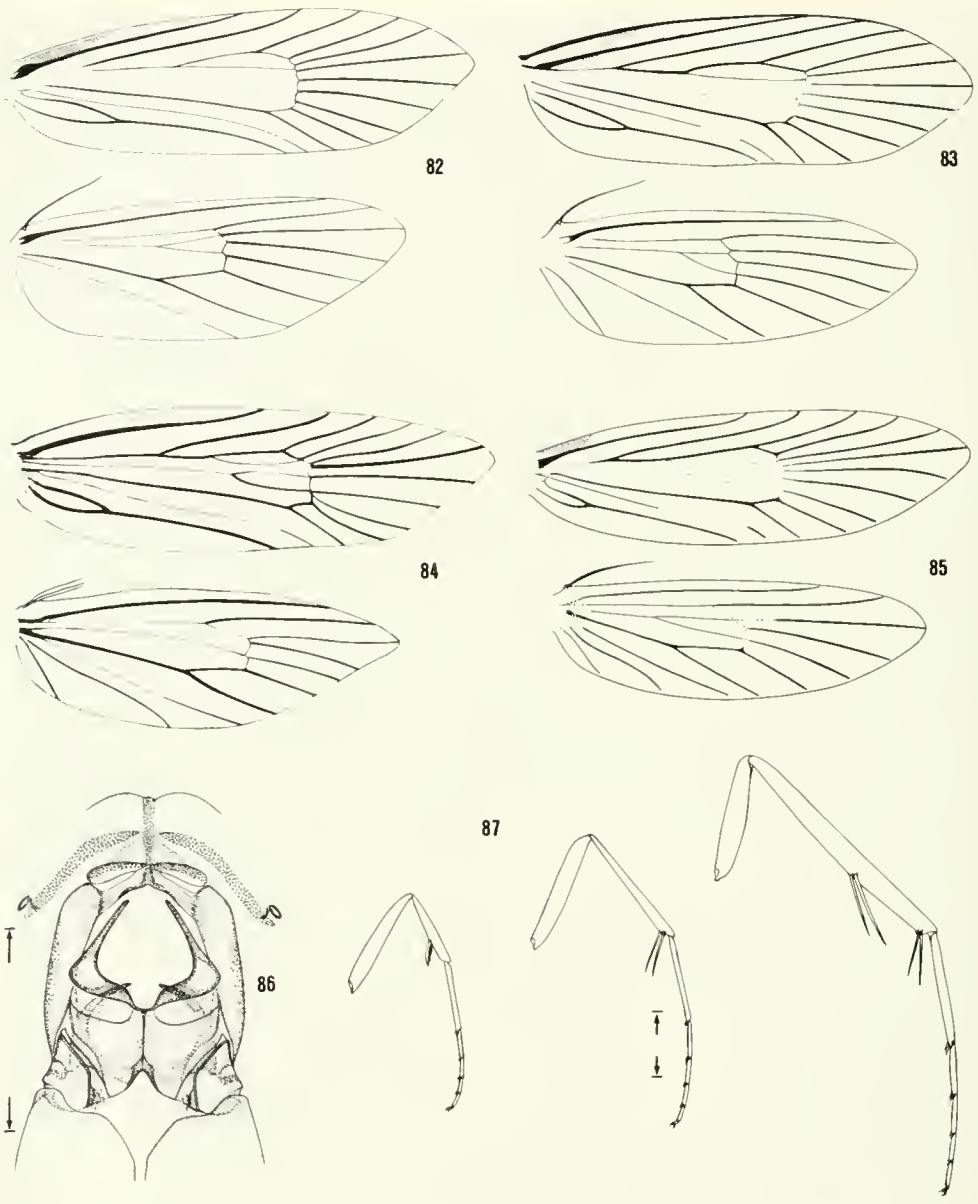

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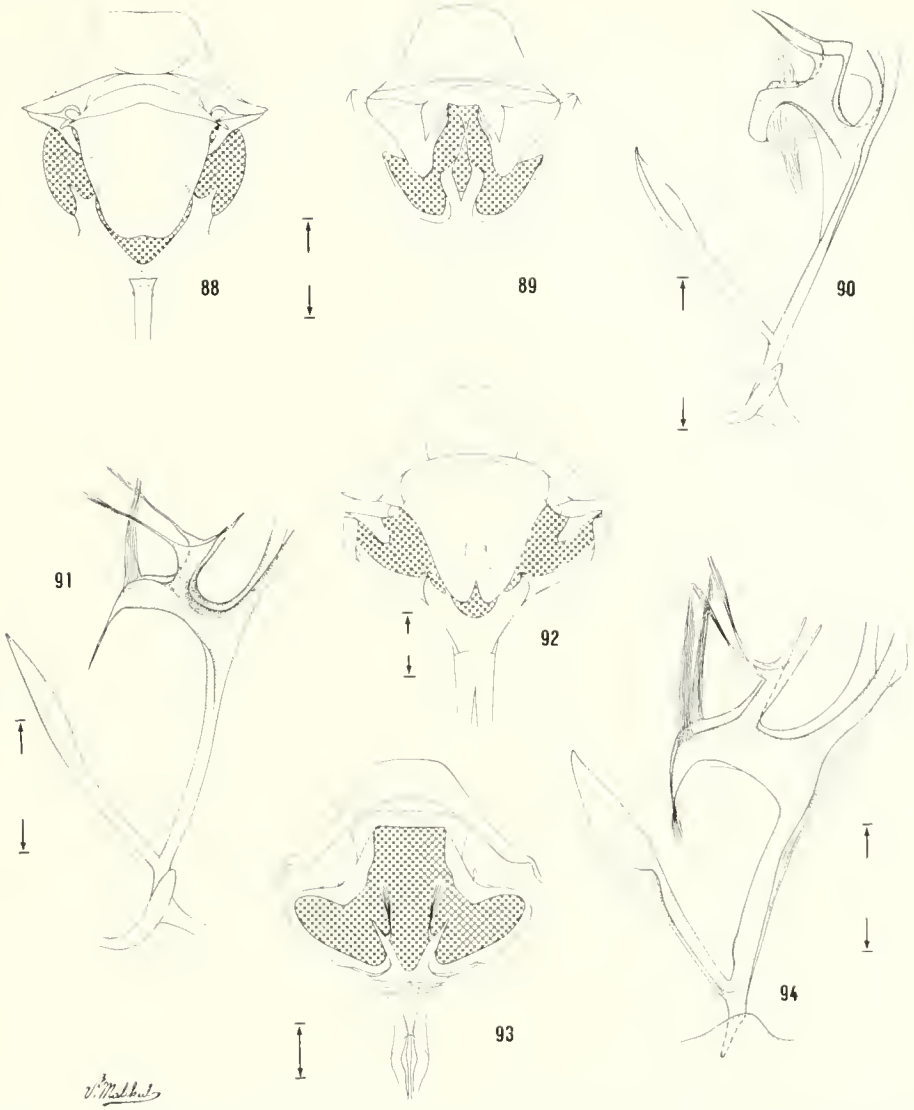
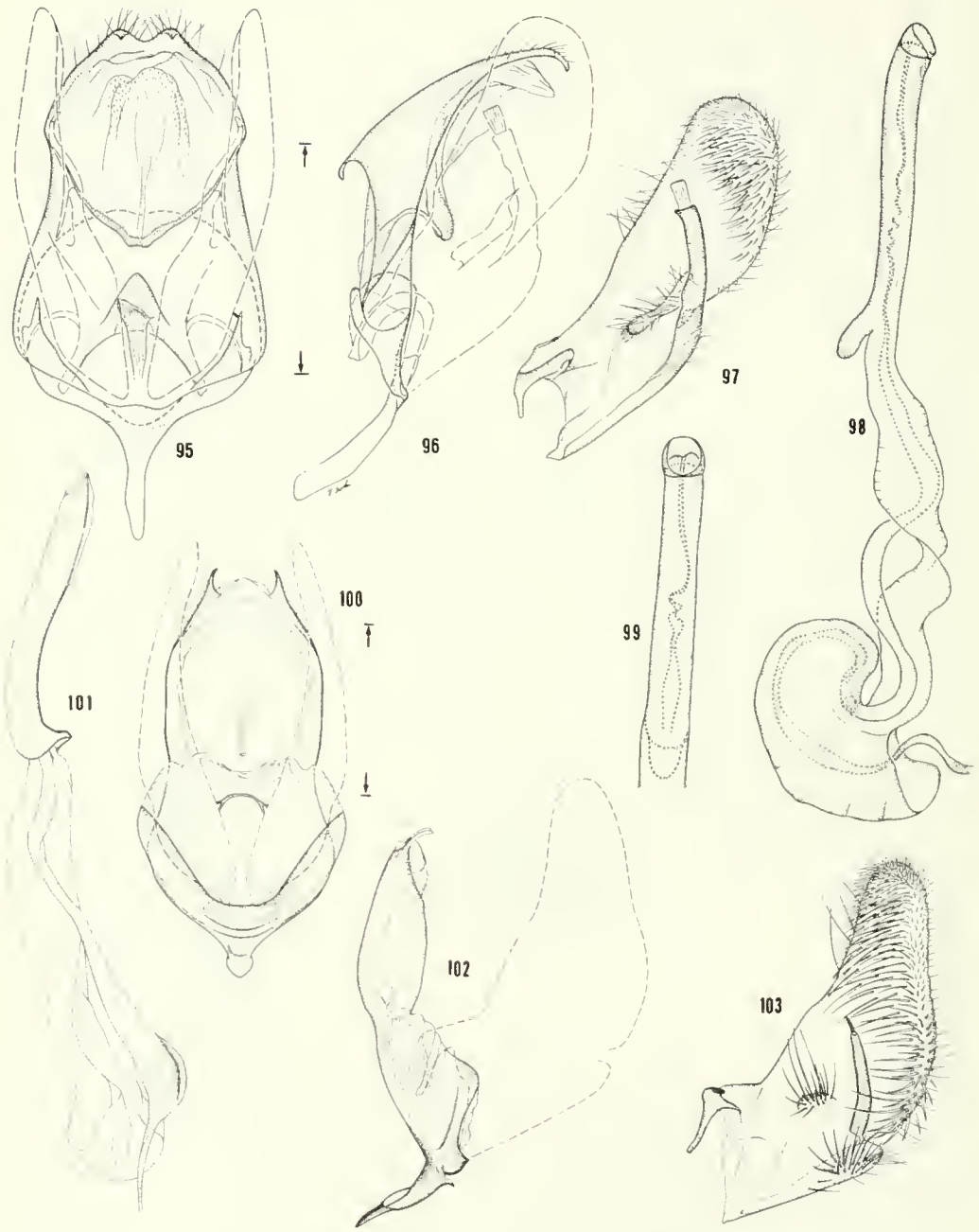


Figs. 88–94. Eriocottidae, thoracic structure. 88, *Crepidochares aridula*, n. sp., posterior view of mesothorax (0.25 mm). 89, Posterior view of metathorax. 90, Lateral view of metafurcasternum (0.25 mm). 91, *Eriocottis fuscanella* Zeller, lateral view of metafurcasternum (0.25 mm). 92, *Compsoctena thwaitesii* (Walsingham), posterior view of mesothorax (0.5 mm). 93, Posterior view of metathorax. 94, Lateral view of metafurcasternum (0.5 mm). (Scale lengths in parentheses.)



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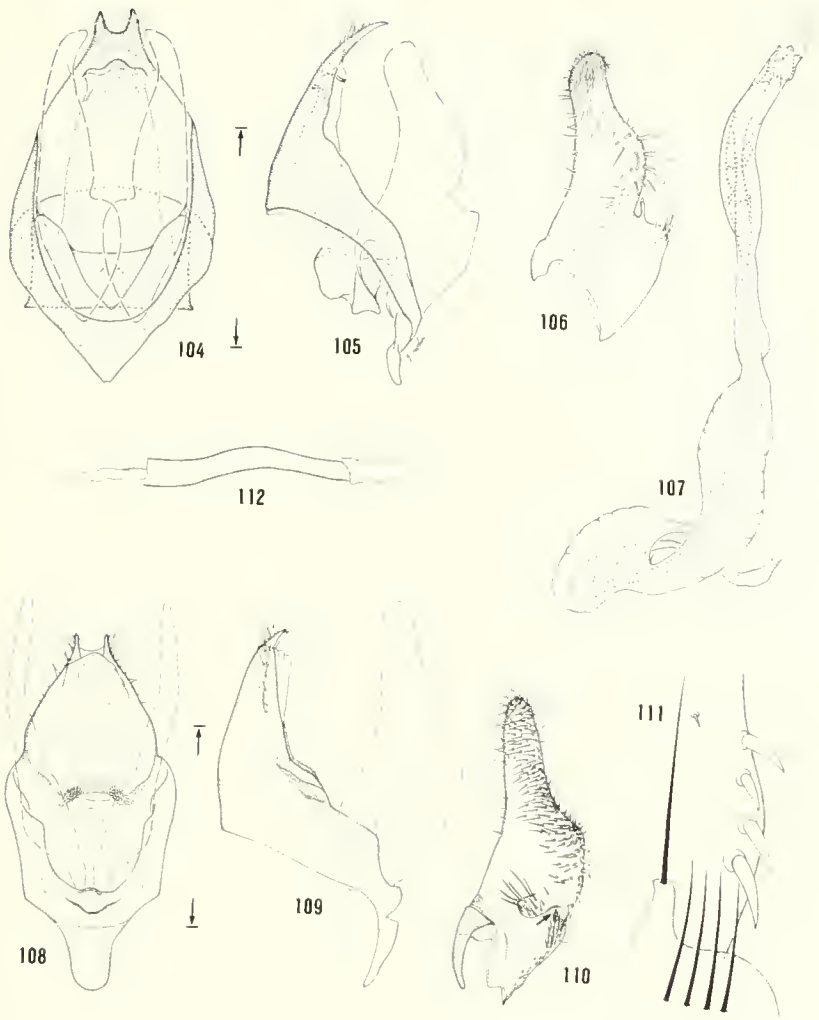

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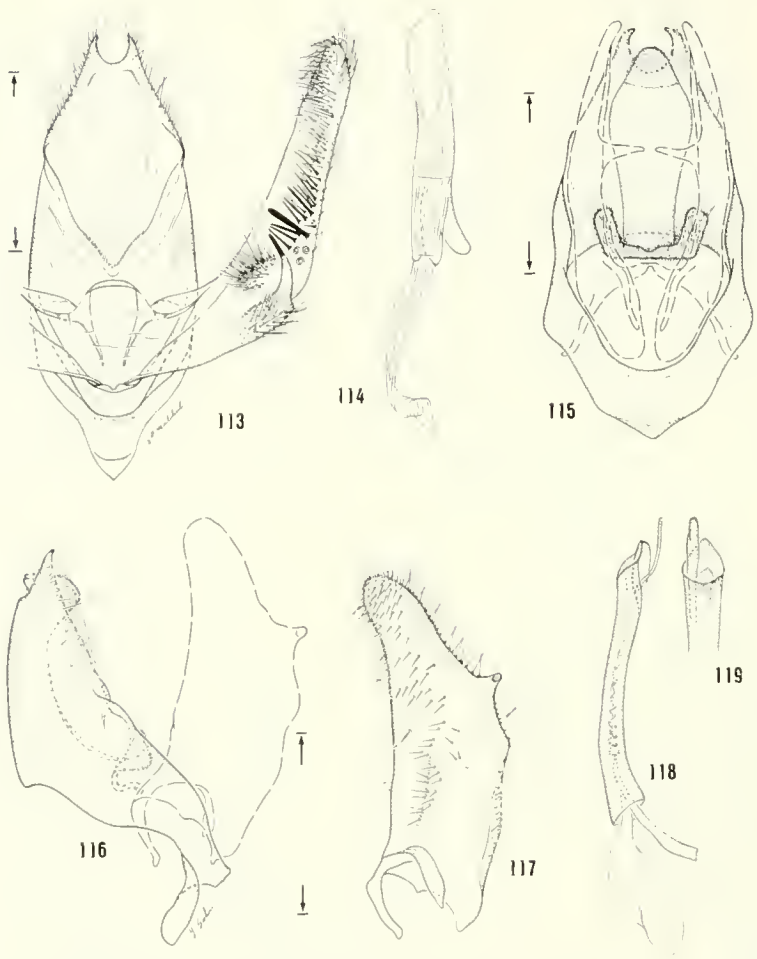
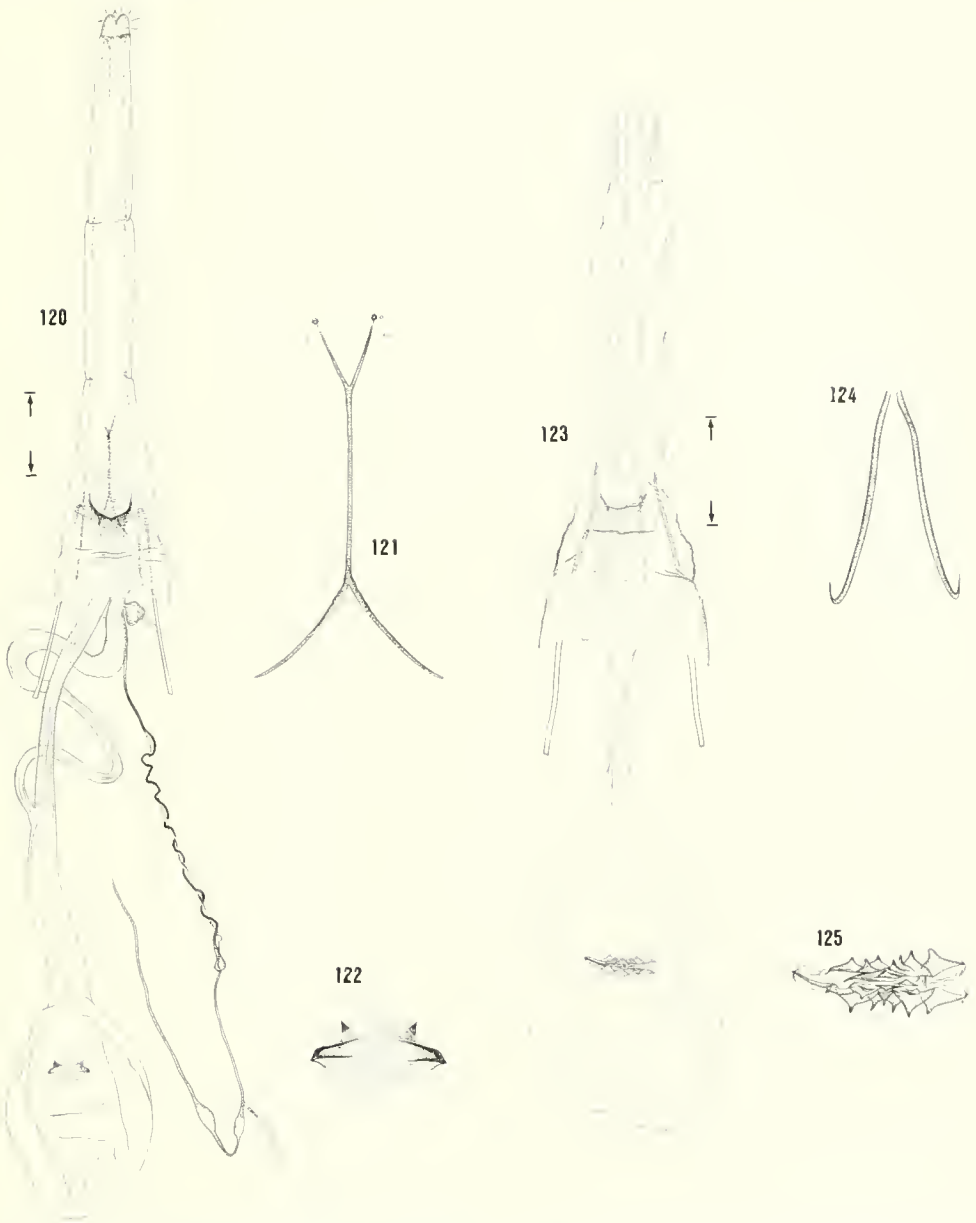
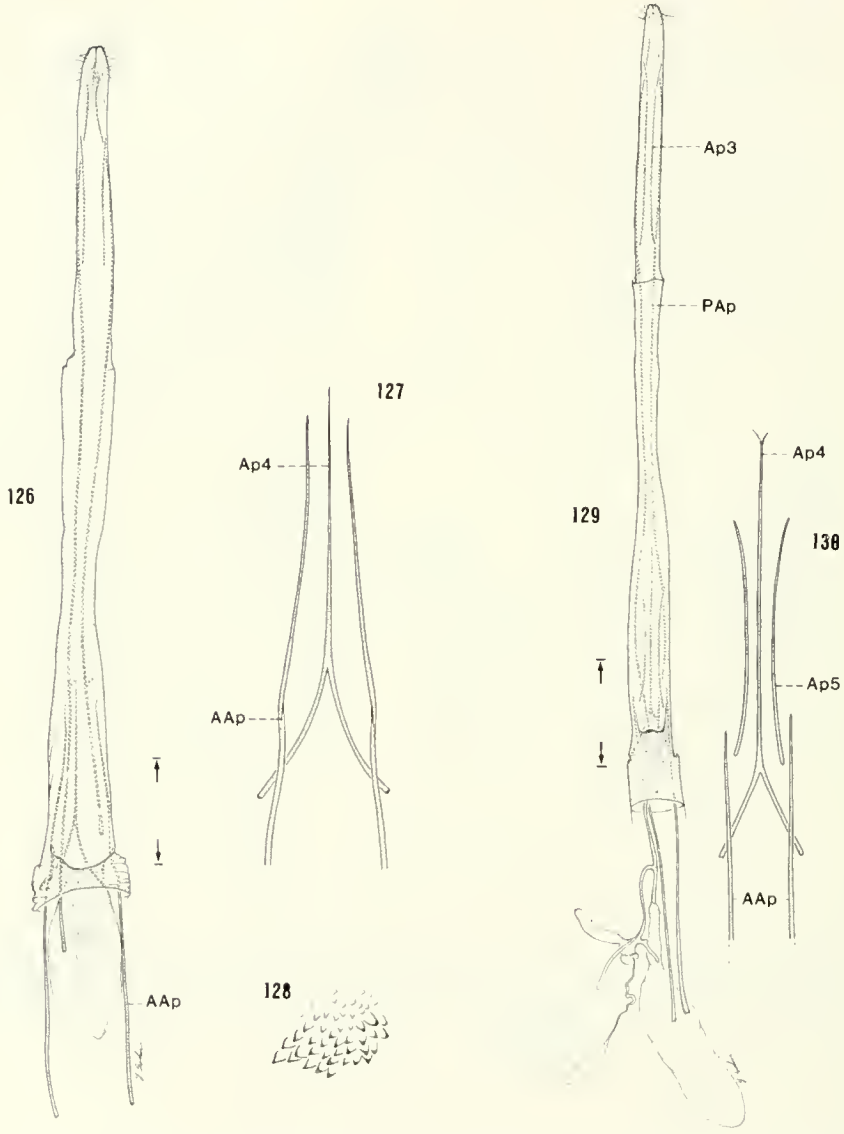


Figs. 113–119. Eriocottidae, male genitalia. 113, *Crepidochares subtigrina* Meyrick, ventral view (0.5 mm). 114, Aedoeagus. 115, *Eriocottis flavicephalana* Issiki, ventral view (0.5 mm). 116, Lateral view of Fig. 115. 117, Lateral view of valva. 118, Aedoeagus, lateral view. 119, Apex of aedoeagus, ventral view. (Scale lengths in parentheses.)



Figs. 120–125. *Crepidochares, female genitalia. 120, Crepidochares neblinae* n. sp., ventral view (0.5 mm). 121, Detail of fourth pair of apophyses. 122, Signum. 123, *Crepidochares colombiae* n. sp., ventral view (0.5 mm). 124, Detail of fourth pair of apophyses. 125, Signum. (Scale lengths in parentheses.)



Figs. 126–130. *Crepidochares*, female genitalia. 126, *Crepidochares austrina* n. sp., ventral view (0.5 mm). 127, Detail of fourth pair of apophyses. 128, Signum. 129, *Crepidochares aridula* n. sp., ventral view (0.5 mm). 130, Detail of fourth (Ap4) and fifth (Ap5) pairs of apophyses. (Scale lengths in parentheses.)

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PHYLOGENETIC REVIEW OF THE *STIROPIUS* GROUP OF GENERA (HYMENOPTERA: BRACONIDAE, ROGADINAE) WITH DESCRIPTION OF A NEW NEOTROPICAL GENUS

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Abstract.—The four New World genera of the *Stiropius* group of rogadine braconid genera are discussed and a cladogram is presented along with supporting characters. The fourth genus, ***Choreborogas*** gen. n., is described with ***C. birostratus*** sp. n. as type-species. A second Neotropical representative of the genus, ***C. andeanus*** sp. n., is also described, to illustrate the range of variation found within the genus.

Key Words: Hymenoptera, Rogadinae, *Stiropius*, phylogeny, character analysis

The generic classification of the tribe Rogadini has long been in need of revision, especially for the non-Holarctic groups. The recent interest in the related tribes Exothecini (van Achterberg 1983; Belokobyl'skii 1984, Papp 1975) and Rhysipolini (Whitfield 1988b; Whitfield & van Achterberg 1987), as well as comparative biological studies of the three tribes (Shaw 1983), now make it possible to begin investigating the Rogadini in a clearer biological and phylogenetic context. This paper, along with Whitfield (1988a), treats the four genera of a moderate-sized group of relatively primitive Rogadini that are confined to the New World. Work is under way on eventually revising all of the species (almost entirely undescribed) of the four genera. The Neotropical faunas of three of the four genera are considerably larger and more abundant than had previously been suspected, probably because many of the species are tiny and nocturnally active.

Materials and Methods

The following institutions and curators supplied specimens used in this study: American Entomological Institute, H. K. Townes (HKT); Canadian National Collection of Insects, Ottawa, M. J. Sharkey (CNC); Rijksmuseum van Natuurlijke Historie, Leiden, C. van Achterberg (RMNH); Texas A&M University, R. A. Wharton (TAMU); R. A. Wharton Collection (RAW); J. B. Whitfield Collection (JBW).

Morphological terminology follows that of Whitfield (1988a) and Whitfield & van Achterberg (1987), except for the use of the term metapostnotal-propodeal groove, which follows Whitfield et al. (1989). All drawings and measurements, with the exception of the wings, were made at 35× or 70× using an ocular micrometer scale and grid, along with squared paper. The wings were slide-mounted in Faure's medium and projected onto a wall and traced.

Phylogenetic analyses made use of the PAUP program (Swofford 1980) to find the shortest trees, and of the MACCLADE program (Maddison & Maddison 1987) to explore the consequences of alternative character polarities and codings.

Morphology and Character Analysis

Ten characters were found especially useful as phylogenetic indicators at the generic

level. These are listed below along with discussion of the alternate states and of character polarities. A matrix of the genera and their character states is provided in Table 1.

1) *Malar (subocular) suture.* Most, indeed nearly all, genera of Rogadinae s.l. possess distinct malar sutures (state 0). Almost certainly the absence of this suture (state 1), as found in *Polystenidea* (Fig. 3) and *Aleiodes*, is derived.

2) *Malar space.* As with character 1, the putative ancestral state 0, a short malar space of half the eye height or less, is widespread, nearly universal, among Rogadinae *s.l.* There are other genera outside the *Stiropius*-group that have long malar spaces, but this feature is not necessarily correlated with loss of the malar suture. In *Polystenidea*, the malar space is long (state 1) but not produced into a rostrum; instead, it is swollen along with the postgenae.

3) *Vein 2Rs of fore wing.* In most Rogadinae that have a distinct 2Rs segment (delimited distally by 2r-m), 2Rs is at least as long as 2r, or nearly so (state 0). The exceptions, including *Artocella* van Achterberg, appear not to be closely related so I have treated them as independently derived conditions. In *Viridipyge* 2Rs is less than half as long as 2r (state 1) and often even reduced to nothing, such that the second cubital cell is triangular.

4) *Vein 2r-m of fore wing.* The presence of this vein (state 0) is ancestral for Rogadinae, indeed for all the cyclostome subfamilies and for the family as a whole. As pointed out by Mason (1981), the loss of this vein can often occur by different means, even among relatively closely related groups. Within the *Stiropius* group of genera, *Polystenidea* and *Choreborogas* have lost this cross-vein (state 1).

5) *Origin of vein r on pterostigma.* The apparent sister-group of Rogadini, the Rhysipolini (see Belokobyl'skii 1984 and Shaw 1983), as well as most Rogadini, have r arising near the midlength of a relatively broad stigma (state 0). The species of *Choreborogas* have r arising relatively proximally on the stigma (state 1), as the result of distal elongation of the stigma. This distal stigmal elongation occurs in some other Rogadinae s.l., e.g. Hormiini and some Exothecini, but is not universal in those groups and the genera concerned are not particularly closely related to Rogadini s.s.

Table 1. Character state matrix for the *Stiropius* group of genera. Characters are described using the same numbers in the text.

Taxa	Characters									
	1	2	3	4	5	6	7	8	9	10
Viridipyge	0	0	1	0	0	1	0	0	0	1
Choreborogas	0	0	0	1	1	1	1	1	0	0
Stiropius	0	0	0	0	0	0	0	1	1	0
Polystenidea	1	1	0	1	0	0	0	1	1	0

6) *Hind femora and tarsomeres.* The biological significance of these modifications is unclear. Generally speaking, the only rogadine genus outside the *Stiropius* group possessing similar leg modifications is *Yelicones* Cameron, which differs so strongly in metasomal structure and wing venation that I cannot think the resemblance is due to common inheritance of the feature. Virtually all species of *Viridipyge* and *Choreborogas* possess swollen hind femora and ultimate tarsomeres (state 1) to some degree, at least on the hind legs of the females.

7) *Posterior width of metasomal T1.* The articulation of T1 and T2 in Rogadini is typically along virtually the entire width of the anterior edge of T2, and T1 broadens posteriorly to meet this width (state 0). In *Choreborogas*, T1 does not broaden appreciably posteriorly, at least not to the extent that it articulates with the anterolateral corners of T2. The result (state 1) is that T2 has anterolateral 'shoulders' extending laterally beyond the edges of T1, giving the metasoma a petiolate appearance.

8) *Metasomal sternite plates.* In virtually all Rogadini s.s. and Rhysipolini s.s., the

metasomal sternites are relatively evenly sclerotized beyond S2 (state 0), although usually not rigid or heavily pigmented. In many Hormiini and some Exothecini, as well as in all of the *Stiropius* group except *Viridipyge*, the sternites (occasionally excepting some posterior ones) are largely desclerotized except for sublateral, pigmented plates (state 1), which usually bear a number of setae. I am forced to regard the medial desclerotization of the sternites in other tribes as independently derived (and in those groups it is accompanied as well by general desclerotization of large portions of the metasoma).

9) *Metasomal tergite IV.* In *Polystenidea* and *Stiropius*, T4 bears a subbasal semicircular groove or depression (state 1), into which, in some stances, the posterior margin of T3 fits. This feature appears to be virtually identical in the two genera and does not appear, to my knowledge, elsewhere. The usual situation is an even, sometimes sculptured, fourth tergite that is capable of being entirely telescoped under T3 (state 0).

10) *Hypopygium.* The usual condition in Rogadini is a short, truncate hypopygium (state 0), except in some of those very few species with long ovipositors. In *Viridipyge*, the hypopygium is more elongate and triangular, such that it projects posteriorly, often beyond the posterior extent of the metasomal dorsum (state 1).

Phylogeny and Classification

Figure 1 depicts the favored cladogram of *Stiropius*-group relationships. PAUP analyses using the ALL TREES option found several alternative possibilities of equal length, but which required unlikely polarities or favoring of weak shared character states (e.g. losses) at the expense of more convincing ones.

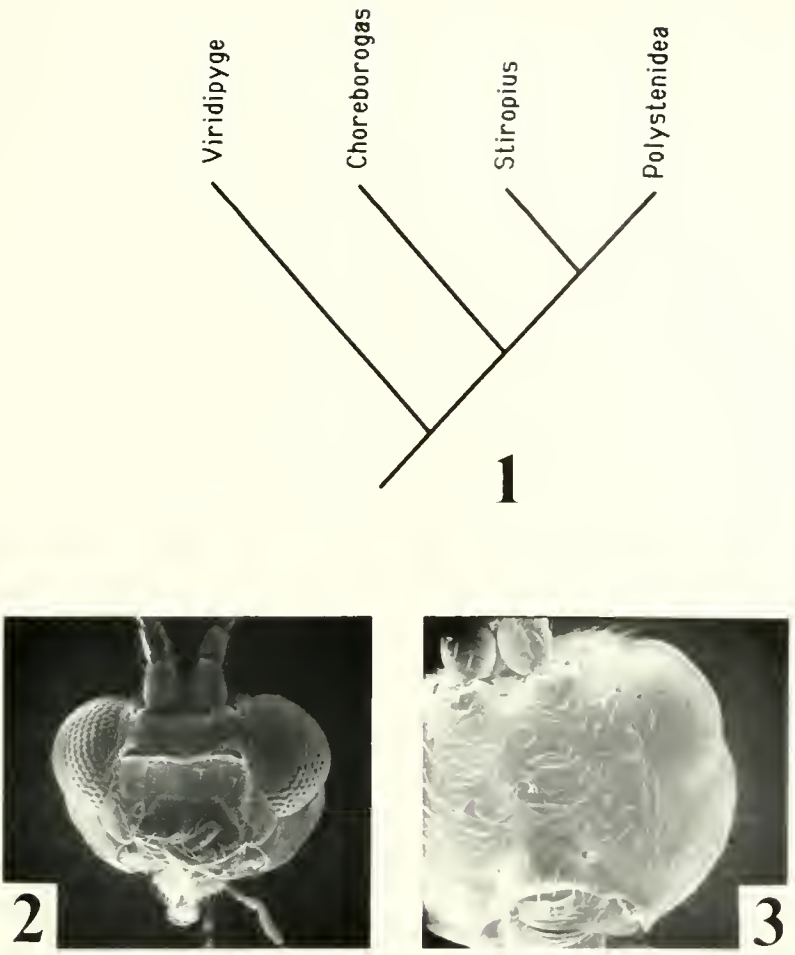
In this scheme, *Viridipyge* is the sister-group of the other three genera, which share the following synapomorphy: metasomal sternites 3–5 desclerotized medially, with sublateral pigmented plates. *Viridipyge* has two autapomorphies: the short 2Rs of the fore wing, and the large, triangular hypopygium. If this cladogram realistically depicts the relationships among the genera, then either a) the swollen hind femora and apical tarsomeres of *Viridipyge* and *Choreborogas* are ancestral for the entire group of genera, or b) they have been independently derived in these two genera.

Choreborogas is then the sister-group of the remaining two genera, which share: metasomal tergite IV with subbasal semicircular groove. Two autapomorphies then characterize *Choreborogas*: T1 much narrower posteriorly than anterior edge of T2 (metasoma subpetiolate), and r arising relatively proximally on a distally elongate stigma. A realistic alternative set of relationships is *Choreborogas* + *Viridipyge* forming a sister group to the other two genera; I have considered the evidence for this alternative, the sharing of the swollen hind femora and tarsomeres, to be weaker than the shared sternite structure of *Choreborogas* + *Stiropius* + *Polystenidea*.

Polystenidea shares (apparently as the result of convergence) with *Choreborogas* the loss of cross-vein 2r-m of the fore wing. It also has two autapomorphies (additionally distinguishing it from *Stiropius*): the elongate malar space and the loss of the malar suture. It is possible that *Stiropius* is paraphyletic with respect to *Polystenidea*; Viereck (1912) noted the extreme similarity in metasomal structure. The addition of more characters to the analysis would help resolve whether the 2r-m loss in *Polystenidea* is an independent development or the cross-vein has been regained in *Stiropius*. As the two genera are amply distinguishable, I prefer not to combine them until the possible paraphyly of *Stiropius* is better established.

Key to the Genera of the *Stiropius* Group of Genera

1 Fore wing vein 2r-m present 2
– Fore wing vein 2r-m absent 3
2 2Rs of fore wing at most two-thirds as long as



Figs. 1–3. 1, Cladogram of *Stiropius* group of genera; 2, face of *C. birostratus*, ♀, anterior view; 3, face of *Polystenidea* sp., anterior view.

2r; hind femora and apical tarsomeres enlarged, swollen; second metasomal tergite at least 1.5× as broad posteriorly as anteriorly; hypopygium triangular in profile, protruding ..... *Viridipyge* Whitfield

– 2Rs of fore wing subequal in length with 2r, sometimes longer; hind femora and apical tarsomeres not enlarged; second metasomal tergite variable but seldom as much as 1.5× as broad posteriorly as anteriorly; hypopygium truncate, short ..... *Stiropius* Cameron

3 Malar suture present and distinct between compound eye and mandibular base (Fig. 2); malar space relatively short, less than half eye height; pterostigma of fore wing almost always elongate distally, so that r arises from stigma well before midlength (Figs. 4, 10); hind femora often swollen or otherwise modified (Fig. 5); metasomal tergite IV without semicircular subbasal groove or depression .. *Choreborogas*, new genus

– Malar suture absent, at least not apparent; malar space long, nearly equal to eye height (Fig. 3); r arising from stigma at about midlength; hind femora not modified or swollen, metasomal tergite IV with semicircular subbasal groove or depression ..... *Polystenidea* Viereck

Choreborogas, gen. n.

Type-species: Choreborogas birostratus, n. sp., described below.

Diagnosis.—This genus shares with the other three related genera the following

combination of features: antennae 13–14 segmented; reduced notauli, especially posteriorly; areolate propodeum; metasomal pseudo-carapace incorporating T1–T3 and, to a lesser extent, T4; ovipositor and sheaths short, partially exserted; gonobase of male subtriangular, nearly as long as broad. There are no really substantiated host records; I expect the hosts, as in the other three genera, are lyonetiid or related leafmining Lepidoptera, and that the wasps endoparasitically mummify the host larvae or prepupae.

Choreborogas differs from *Polystenidea* in lacking the semicircular, subbasal groove on the fourth metasomal tergite, in having an apically elongate pterostigma (as in *Chorebus*, hence the generic name), in having distinct malar or subocular sutures and in often having swollen hind femora and apical tarsomeres. It is also distinguished from *Stiropius* by all of the above differences except the subocular sutures, as well as by lacking vein 2r-m of the fore wing. Finally, it differs from *Viridipyge* in possessing sublateral, pigmented, more strongly sclerotized plates on metasomal sterna 2–5, in having the apically elongate pterostigma, and in lacking the vein 2r-m of the forewing.

Stiropius and *Viridipyge* will both key to *Bucculatriplex* in Marsh et al. 1987; *Polystenidea* and (sometimes with great difficulty) *Choreborogas* will key to *Polystenidea*.

Comments.—As far as is known, the species of *Choreborogas* are all predominantly Neotropical, with several of the species ranging into the southeastern U.S. and probably into parts of Arizona as well. They are quite abundant in some light trap samples from Central America, indicating that they are probably nocturnally active and often numerous. I have seen an estimated 20 species in collections. Two new species, the first being the type, are described below to illustrate the range of features found in this remarkable, yet essentially unknown, group of wasps.

***Choreborogas birostratus*, sp. n.**
Figs. 2, 4, 5, 6, 7

Female.—*Body length:* 1.4–2.1 mm, fore wing length 1.6–2.4 mm.

Head: Color orange-brown, often with darker brown regions around ocelli, facial carinae and occipital carina. Supraoral depression enlarged to include lower 0.3–0.5 of frons; clypeus embedded within this depression and flattened; depression marked dorsally and laterally by carina, which is produced submedially into two flattened pointed noselike projections. Mandibles enlarged and strongly overlapping when closed. Inner margins of eyes parallel to diverging ventrally. Malar space less than 0.3 eye height, with strong malar suture. Antennae 14-segmented, slightly shorter than body, with apical flagellomeres 3–4× as long as broad. Maxillary and labial palpi pale yellowish, slender. Hypostomal and occipital carinae remaining separate to mandibular bases. Ocelli roughly equidistant from each other.

Mesosoma: Entirely pale orange-brown (occasionally darker brown in generally darker specimens). Pronotum with shallow, narrow dorsal and ventral grooves, otherwise nearly smooth. Mesoscutum very finely granular, matte, with weak indentations indicating courses of notauli. Scutoscutellar scrobe composed of two transverse excavations, narrower medially and traversed medially by a thin ridge. Scutellar disc finely punctate, flat. Mesopleuron weakly granular, with shallow, sinuate logitudinal groove. Propodeum with narrow but distinct metapostnotal-propodeal groove, medial longitudinal carina over anterior 0.4–0.5, and posterior medial gothic-arch-shaped areola; costulae obsolescent or entirely absent.

Wings: C+Sc+R and stigma pale yellow-brown; stigma occasionally whitish in some specimens. Remainder of prominent venation evenly brownish. Fore wing (Fig. 4) with r originating in basal 0.3–0.4 of stigma,

2r-m absent. Stigma 4× as long as broad. 3Rs meeting wing edge about 0.6 of distance between distal end of stigma and wing tip, just short of end of R1 (metacarp).

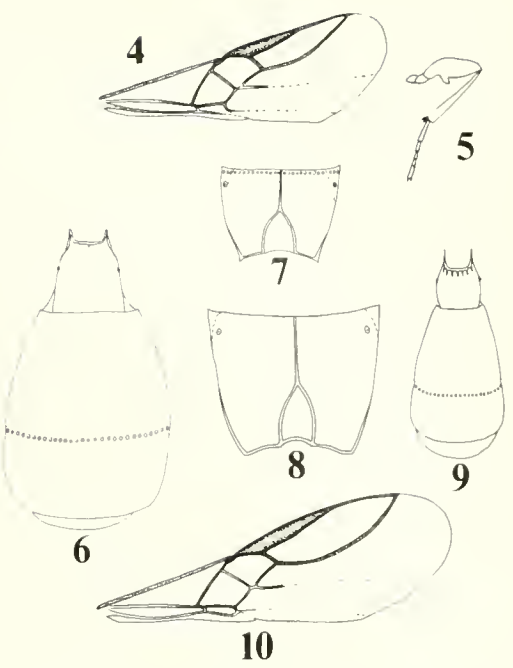
Legs: All legs pale yellow-brown with ultimate tarsomeres dark brown apically. Hind femora (Fig. 5) swollen, each with subbasal ventral toothlike projection. Hind tibiae armed with considerably longer setae than remainder of legs. Front and hind apical tarsomeres enlarged, about 2× as broad as preceding tarsomeres.

Metasoma (Fig. 6): T1, T2, anterior edge of T3 light orange-brown and mostly with granular sculpturing. T3 and T4 darker brown. Tergite 1 weakly broadening posteriorly, about 1.3× as long as posteriorly broad, with semicircular basal carina and longitudinal medial carina. T2 1.4× as broad posteriorly as long, 1.6× as broad posteriorly as anteriorly, separated from T3 by crenulate furrow. T2 1.5× as broad as T1 at junction with T1. T3 2× as broad as long, weakly rounded posteriorly and strongly overlapping T4. T4 much narrower than T3, anteriorly transversely striate, posteriorly granular. Hypopygium short, truncate, not projecting. Ovipositor and sheaths short, subexserted.

Males.—Essentially same size range as females but with some pronounced morphological differences: lower portion of frons not incorporated into large supraoral depression (thus facial carinae and projections are absent); mandibles not enlarged apically; stigma broader (3× as long as broad); hind femora less strongly swollen and without subbasal, ventral toothlike projection.

Material examined.—*Holotype* ♀: MEXICO: Guerrero, 17 mi. E. Tixtla, 11.vii.1985 (*Woolley, Zolnerowich*) (TAMU, deposited in USNM). *Paratypes*: MEXICO: Colima: 1 ♂, Parque Nac. de Volcan Colima, 8.2 mi. from Hwy. 54, 12.vii.1984 (*Woolley*) (TAMU). Guerrero: 3 ♀, same data as holotype; 1 ♀, 3 ♂, 6 mi. E. Xochipala, 13.vii.1985 (*Woolley, Zolnerowich*) (TAMU); 4 ♀, 3 ♂, 6.2 mi. SW Xochipala, 13.vii.1985 (*Woolley, Zolnerowich*) (TAMU); 1 ♂, 2 mi. E. Ocotito, 11.vii.1985 (*Woolley, Zolnerowich*) (TAMU); 1 ♀, 32 mi. SE Petatlan, 10.vii.1985 (*Woolley, Zolnerowich*) (TAMU). Michoacan: 1 ♀, 49 mi. SE Aguila, 13.vii.1984 (*Woolley, Zolnerowich*) (TAMU); 1 ♀, 28.5 mi. S. Nueva Italia, 9.vii.1985 (*Woolley, Zolnerowich*) (TAMU); 1 ♀, 10 mi. S. Uruapan, 7.vii.1985 (*Woolley, Zolnerowich*) (TAMU). Oaxaca: 1 ♀, 4.4 mi. NE San Pedro Mixtepec, 16.vii.1985 (*Woolley, Zolnerowich*) (TAMU). Tamaulipas: 2 ♀, 5 ♂, 5 mi. W. Gomez Farias, 20.iii.1986 (*Wharton*) (RAW, deposited in USNM).

Comments.—This species is as remarkable for its pronounced sexual dimorphism



Figs. 4–10. 4, Fore wing of *C. birostratus*, sp.n., ♀; 5, hind leg of *C. birostratus*, sp. n., ♀; 6, metasomal tergites of *C. birostratus*, sp. n., ♀; 7, propodeum of *C. birostratus*, sp. n., ♀; 8, propodeum of *C. andeanus*, sp. n., ♀; 9, metasomal tergites of *C. andeanus*, sp. n., ♀; 10, fore wing of *C. andeanus*, sp. n., ♀.

as for its unusual facial features. At least one other undescribed species from Central America shares a similar facial modification (along with even more extreme modifications of the hind legs), but many species are similar to *C. birostratus* males in both sexes. This species can be easily separated from the following one by the shape of the metasomal tergites (Fig. 6), the small size (usually less than 2 mm), the distally less elongate fore wings, as well as by the striking modifications of the face and hind femora in the females.

***Choreborogas andeanus*, sp. n.**
Figs. 8, 9, 10

Females.—*Body length:* 2.0–2.4 mm; fore wing length 2.7–3.1 mm.

Head: Entirely deep brown except light yellow-brown labrum, mandibles and palpi. Supaoral depression round, small; clypeus apically concave. Frons finely granular; inner margins of eyes parallel. Antennae 14-segmented, apical 5 flagellomeres more terete. Malar spaces about 0.3 eye height, with strong malar suture. Ocelli roughly equidistant from each other.

Mesosma: Mostly weakly punctate/granular dorsally, shinier laterally, entirely deep brown. Pronotum smooth, polished, with narrow, shallow dorsal and ventral grooves. Mesoscutum with no sign of notauli, evenly and finely punctate. Scutoscutellar scrobe composed of two broad rectangular excavations separated by a narrow ridge. Scutellar disc sculptured as mesoscutum, weakly convex, subtriangular. Mesopleuron highly polished, with very faint to absent longitudinal depression. Propodeum (Fig. 8) with narrow but distinct metapostnotal-propodeal groove, medial longitudinal carina over anterior 0.5–0.6, and horseshoe-shaped to narrower pointed medial areola posteriorly. Costulae absent.

Wings: Wings disproportionately large relative to body size. Venation entirely pale brownish. Fore wing (Fig. 10) with apically extremely elongate stigma (stigma 7× as long as broad), r arising in its proximal 0.2. 3Rs strongly curved, reaching wing margin approximately halfway between distal end of stigma and wing tip.

Legs: All legs pale yellow-brown with darker, strongly swollen ultimate tarsomeres. Hind femora swollen but otherwise unmodified, with sparse setae of average length.

Metasoma (Fig. 9): Tergite 1 finely punctate, 1.3× as long as posteriorly broad, weakly broadening to spiracle then parallel-sided, with semicircular carina anteriorly and obsolescent medial longitudinal carina. Tergite 2 finely granular, 1.5× as broad at T1/T2 junction as T1, slightly longer than apically broad, separated from T3 by shallow, crenulate groove. T3 smooth, polished, 1.9× as broad as long, with strongly rounded posterior margin. T4 and succeeding tergites smooth, more flexible, telescoped under T3. Hypopygium short, truncate, not projecting ventrally. Ovipositor and sheaths short, subexserted.

Males.—Essentially similar to females, but with slightly more parallel-sided T2 and relatively less transverse T3, which tends to have more (albeit weak) sculpturing as opposed to the smoother T3 in the female.

Material examined.—*Holotype* ♀: COLOMBIA: Putumayo, 2900 m, 1°10′N, 77°15′W, 2.xii.1972 (*Helava*) (CNC). *Paratypes:* 1 ♀, 6 ♂, same data as holotype; COLOMBIA: Antioquia, 1 ♀, 1800 m, 7°5′N, 76°30′W, (no date) (*Helava*) (CNC); Quindio, 1 ♀, 11 km E. Calarca, 7000′, 5.iii.1974 (*Peck & Peck*) (CNC). PERU: Amazonas, 1 ♂, 2800 m, 6°48′S, 77°38′W, 13.ii.1973 (*Helava*) (CNC).

Comments.—At first glance, the peculiar long-winged and polished appearance of this species makes it seem entirely unrelated to *C. birostratus*. In many structural features, however, the two species are quite similar, one or the other being more extreme in some respect. The peculiar appearance of both species is produced by exaggeration of tendencies found in most species of the genus

to some degree. It would be quite interesting to know what advantage, if any, the long wings of *C. andeanus* confer.

Acknowledgments

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DESCRIPTIONS, DISTRIBUTION, AND HOST-PLANT RECORDS OF EIGHT FIRST INSTARS IN THE GENUS *TOUMEYELLA* (HOMOPTERA: COCCIDAE)

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Abstract.—Detailed morphological descriptions of first-instar nymphs of 8 species in the genus *Toumeyella* are presented. Included are illustrations, a key to described species, and discussions of general morphology and species relationships. The first instar of a ninth species *T. sonorensis* (Cockerell and Parrott), historically included in the genus, proved not to be congeneric with the type or other species within the genus. Host plants and distributions are also given.

Key Words: Homoptera, Coccoidea, Coccidae, *Toumeyella*, first instars

The soft scale insect genus *Toumeyella* was first proposed as a subgenus of *Lecanium* Burmeister by Cockerell in 1895 with *Lecanium mirabile* as its type species. Cockerell (1902) later elevated it to generic rank. As currently recognized, the genus *Toumeyella* is composed of 11 described species, 8 of which occur in North America.

Identification of species of *Toumeyella* has been a problem because of a lack of adequate descriptions and keys, as well as apparent host induced and geographical variation in some species. Williams and Kosztarab (1972) and Hamon and Williams (1984) provided descriptions, illustrations, hosts, distributions and biological notes on 5 species occurring in Virginia and Florida, respectively. Included were *Toumeyella cerifera* Ferris, *T. liriodendri* (Gmelin), *T. parvicornis* (Cockerell), *T. pini* (King), and *T. virginiana* Williams and Kosztarab.

Previous taxonomic studies of *Toumeyella* species have focused primarily on adult females, with little attention to other developmental stages. Ferris (1919), in a redescription of *T. mirabilis* (Cockerell), illustrated the first instar in some detail and commented on the spiracular setae, marginal setae, and anal plate reticulation. Heidel and Kohler (1979) presented a brief description and illustration of the first instar of *T. cubensis* Heidel and Kohler. These papers represent the only attempts of describing and illustrating immature stages of *Toumeyella*.

Studies of immature stages of Coccidae are needed to develop complete and sound classification, yet relatively few such studies have been conducted (Howell and Tippins 1973). Classification based solely on adult female characters may produce erroneous phylogenies. For example, the genera *Chionaspis* and *Pseudaulacaspis* were considered closely related until examination of second instar males revealed characters that indicated the genera arose from separate phylogenetic stocks (Takagi and Kawai 1967).

Additionally, extreme host-induced dimorphism can lead to erroneous classifi-

cation. For example, individual *Chionaspis nyssae* Comstock feeding on two different hosts exhibited such diverse morphological characters that they were placed in separate genera (Knipscher et al. 1976). Mobile, nonfeeding first instars are not so influenced by their host as are later developmental stages (Howell 1981). Sibling species and species in complexes may so closely resemble each other as adult females that utilization of immature stages is the only means of separation (Howell 1981). More accurate phylogenies may be produced with the aid of first instar nymphs which exhibit characters often lost or reduced in adult females.

Presented in this paper are detailed descriptions, illustrations and an identification key to first-instar nymphs of 8 species of *Toumeyella*. Distribution and host plant information are given. A discussion of first-instar general morphology, as well as species relationships, is included. The species of *Toumeyella* treated herein occur in North America except *T. nectandrae* Hempel, which is found in Brazil. Three species could not be studied for lack of specimens: *T. cubensis* Heidel and Kohler, a Cuban species; *T. paulista* Hempel, a Brazilian species; and *T. pinicola* Ferris, from the Western United States.

Materials and Methods

Specimens (slide mounted and/or dry) were borrowed from the following institutions: Auburn University (AUEM), Florida State Collection of Arthropods (FSCA), University of California Davis (UCDC), United States National Museum of Natural History (USNM), and Virginia Polytechnic Institute and State University (VPIC).

A minimum of 10 slide-mounted first-instar nymphs were measured for each species description. Measurements were made utilizing a phase-contrast microscope fitted with an ocular micrometer. For each structure measured, the mean and range (parenthetic) are given in microns in each species description. Terminology used in descriptions is from Williams and Kosztarab (1972). Drawings are not made to the same scale in all species nor are dermal structures and enlargements in direct proportion to each other. The scale bar shown in each figure refers only to body size and not to enlargements.

In the Specimens Studied section, the first number indicates the number of slides and the second number (parenthetic) the number of specimens, if different. Collection abbreviations are utilized to indicate specimen deposition in the Specimens Studied section.

General Morphology of First Instar Nymphs

Fig. 1

Body (Fig. 1-A).—Slide-mounted specimens generally oval to elongate-oval, 597 (330–965) long and 354 (215–681) wide. Derm membranous throughout. Appendages, mouthparts, pores and microducts sclerotized. Segmentation.—Head, thorax and abdominal segments closely fused. Segmentation not readily apparent. Antennae (Fig. 1-B).—Antennae well developed, 5-segmented, 3rd and 5th segments generally about equal length. Slender hairlike setae on all segments, with enlarged "stout" sensory setae (Fig. 1-C) on segments 4 and 5. A simple sensory pore (Fig. 1-D) on segment 2. Eyes (Fig. 1-E).—Located on margin just above antennal scape, reduced to a single facet. Mouthparts (Fig. 1-F).—Mouthparts lie between the procoxae, consisting of clypeolabral shield, one-segmented labium with 6–8 setae, and stylet loop. Legs (Fig. 1-G).—Well developed, without tibiotarsal sclerotization or free articulation. Two sensory pores (Fig. 1-H) on each side of trochanter. Various hairlike setae on each segment, and knobbed digitules in pairs on tarsi (Fig. 1-I) and claws (Fig. 1-J) except prothoracic legs with 1 tarsal digitule setiform. Microctenidia (Fig. 1-K) at tibial apex present or absent. Tarsal claw (Fig. 1-L) simple or with a denticle. Spiracles (Fig.

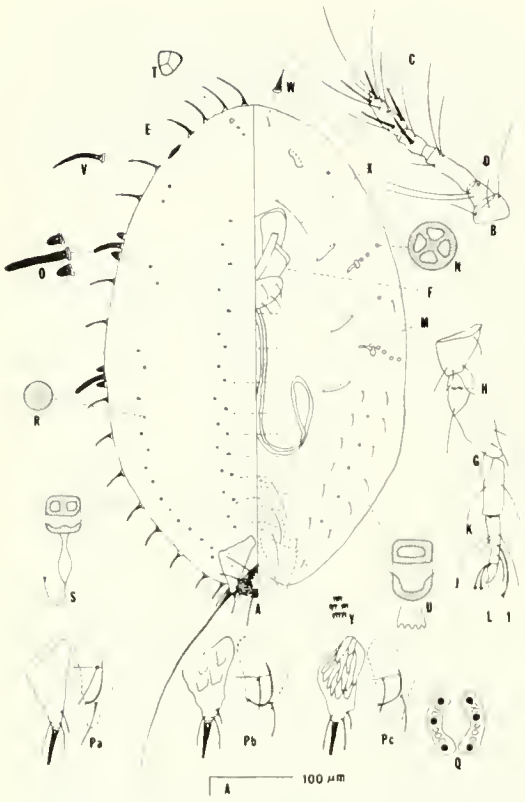

Fig. 1. General morphology, *Toumeyella* first instar.

1-M).—Two thoracic pairs, associated with ventral quadralocular pores (Fig. 1-N) in spiracular furrows; 2–3 pores anteriorly, 3–4 posteriorly. Occasional quinquelocular or 6-locular pore. Spiracular setae (Fig. 1-O).—Three stout spiracular setae in each spiracular furrow in all species except *T. parvicornis* (Fig. 6). Spiracular setae are taxonomically important in separating species. Anal plates (Fig. 1-Pa–c).—Two anal plates, well developed, triangular with rounded angles. Dorsum with surface microspines (Fig. 1-Pa), coarse (Fig. 1-Pb) or dense (Fig. 1-Pc) reticulation. Four dorsal setae per plate; 1 on mesal margin, 3 apical. Thick median apical seta approximately ½ body length. One ventral subapical seta per plate and 1 pair fringe setae on anal fold. Dorsal surface texture of anal plates important in separating species. Anal ring (Fig. 1-Q).—Subcircular to roundly hexagonal with 6 stout anal ring hairs and a row of irregularly shaped pores. Pores.—Small (2 μm dia.), usually simple, dorsal disc pores (Fig. 1-R) in submedian and submarginal longitudinal rows. Dorsal bilocular pores (Fig. 1-S) in submedian and often submarginal longitudinal rows. Bilocular pores categorized as small (longest length 2 μm) to large (longest length 4–8 μm). Dorsal trilocular pore (Fig. 1-T) on derm, anterior to each antennal scape. Ducts.—Ventral microducts (Fig. 1-U) in 2 submarginal longitudinal rows of 5 each on the abdomen, 1 between anterior and posterior spiracular furrows and 1 posterior to each eye. Body setae.—Marginal setae (Fig. 1-V) slender to stout, distribution: 8 anteriorly between eyes, 2–3 on each side between eye and anterior spiracular setae, 2–3 on each side between anterior and posterior spiracular setae, 16 posteriorly on abdomen. Additionally, *T. parvicornis* has 2 setae on the body margin at the apex of each spiracular furrow, which are undifferentiated from marginal setae. Ventral body setae bristlelike, of 2 lengths: submarginal setae (Fig. 1-W) short, in 2 longitudinal rows of 7 each on abdomen, 1 seta between anterior and posterior spiracular furrows and 1 pair at head apex; body setae (Fig. 1-X) long, in 2 submedian rows of 3 each on posterior abdominal segments; with 2 interantennal setae. Other structures.—Ventral microspines (Fig. 1-Y) on posterior abdominal segments.

Key to 8 First-Instar Nymphs of the Genus *Toumeyella*

1. Dorsal bilocular pore clusters present (Fig. 6-C); 44 marginal setae around body; spiracular setae undifferentiated from marginal setae (Fig. 6-B) ..... *T. parvicornis*

1′. Dorsal bilocular pore clusters absent; 32–36 marginal setae around body; spiracular setae distinctly different from marginal setae, 3 in each spiracular furrow (Fig. 1-O) 2

2.(1′) Body with 36 slender marginal setae (Fig. 2-B) ..... *T. cerifera*

2'. Body with 32 slender to stout marginal setae 3

3.(2') Dorsal bilocular pores (2 μm) present in 2 submedian longitudinal rows only (Fig. 4-D); median spiracular setae 5–6 times longer than anterior set of lateral spiracular setae (Fig. 4-C); marginal setae stout ..... *T. mirabilis*

3'. Dorsal bilocular pores (2–8 μm) present in submarginal and submedian longitudinal rows (Fig. 1-S); median spiracular setae approximately 2 times longer than lateral spiracular setae 4

4.(3') Small dorsal bilocular pores (2 μm) present in submarginal and submedian longitudinal rows; tibial microctenidia present (Fig. 1-K) 5

4'. Larger dorsal bilocular pores (>3 μm) present in submarginal and submedian longitudinal rows, predominantly bow shaped (Fig. 8-D); tibial microctenidia absent ..... *T. quadrifasciata*

5.(4) Dorsal bilocular pores (2 μm) present in submarginal, submedian, and intermediate longitudinal rows (Fig. 9-D) ..... *T. virginiana*

5'. Dorsal bilocular pores (2 μm) present in submarginal and submedian longitudinal rows only 6

6.(5') Dorsum of anal plates densely reticulated (Fig. 1-Pc); marginal setae stout; not on *Pinus* sp. 7

6'. Dorsum of anal plates not reticulated, but with sparsely distributed microspines (Fig. 7-H); marginal setae slender (Fig. 7-B); on *Pinus* sp. ..... *T. pini*

7.(6) Dorsal quinquelocular disc pores (2 μm) usually present in submarginal and submedian longitudinal rows (Fig. 3-E); North American ..... *T. liriodendri*

7'. Dorsal quinquelocular disc pores absent; dorsal disc pores simple (Fig. 5-E); Brazilian ..... *T. nectandrae*

Toumeyella cerifera Ferris
Fig. 2

Toumeyella cerifera Ferris 1921: 90. Steinweden 1929: 227, Williams and Kosztarab 1972: 160, Hamon and Williams 1984: 117.

Specimens studied.—*Cephalanthus occidentalis*: 3(13), Sussex Co., Airport Pond, Wakefield, VA, 16 Aug 1969, Michael L. Williams (AUEM); 1, Macon Co., AL, 31 May 1975, MLW (AUEM); 2(8), Macon Co., AL, 21 Jun 1975, MLW (AUEM); 2(21), Macon Co., AL, 13 Jul 1975, MLW (AUEM); 1(3), Macon Co., AL, 24 Aug 1975, MLW (AUEM); 1(2), Macon Co., AL, 13 Oct 1975, MLW (AUEM).

Fig. 2. First instar, *Toumeyella cerifera* Ferris 1921.

Additional host plants and distribution.—*Toumeyella cerifera* was first described from *Albizzia occidentalis* collected in Baja California, Mexico. Reported to occur in AR, FL, LA, and NC.

General appearance.—Body (Fig. 2-A) oval, 642 (514–939) long, 391 (296–610) wide. Dorsum.—Marginal setae (Fig. 2-B) 14 (10–19) long, slender, curved posteriorly, distribution: 8 anteriorly between eyes, 3 on each side between eyes and anterior spiracular setae, 3 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 2-C) in each spiracular furrow; median setae 24 (19–28) long, lateral setae 14 (11–18) long. Small (2 μm) bilocular (Fig. 2-D) and simple disc (Fig. 2-E) pores in submedian and sub-

marginal longitudinal rows. Anal plates (Fig. 2-H).—Each plate with dorsum densely reticulated, 68 (59–78) long, 34 (28–42) wide; cephalolateral margin 44 (40–48) long, caudolateral margin 41 (28–47) long. Venter.—Antennae (Fig. 2-L) 170 (157–179) long. Legs (Fig. 2-M) 250 (234–268) long, microctenidia (Fig. 2-N) at tibial apex; tarsal digitules (Fig. 2-O) 49 (42–56) and 35 (32–37) long; claw digitules (Fig. 2-P) 23 (17–26) long; claws (Fig. 2-Q) with denticle. Diagnosis.—Thirty-six marginal setae occur only in *T. cerifera* and serve to separate it from all other *Toumeyella*. Forty-four marginal setae are found in *T. parvicornis*, and all other species possess 32 marginal setae.

Toumeyella liriodendri (Gmelin)
Fig. 3

Coccus liriodendri Gmelin 1789: 2220.
Lecanium tulipiferae Cook 1878: 192.
Lecanium liriodendri (Gmelin). Cockerell 1899: 271, Herrick 1911: 12, Carnes 1906: 40.
Eulecanium tulipiferae (Cook). King 1902: 59.
Eulecanium (?) *liriodendri* (Gmelin). Fernald 1903: 190.
Lecanium (*Toumeyella*) *liriodendri* (Gmelin). Pettit and McDaniel 1920: 10.
Toumeyella liriodendri (Gmelin). Sanders 1909: 447, Jarvis and Guelph 1911: 70, Dietz and Morrison 1916: 249, Houser 1918: 301, Berger 1922: 68, Harned 1923: 26, Hollinger 1923: 63, Merrill and Chaffin 1923: 273, Trimble 1925: 6, Wells 1926: 257, Trimble 1928: 44, Steinweden 1929: 227, Felt and Rankin 1932: 460, Doane et al. 1936: 380, Dodge and Rickett 1943: 407, Craighead 1950: 144, Milliron 1959: 28, Pirone et al. 1960: 473, Burns 1970: 1, Burns and Donley 1970: 228, 1971: 532, Donley and Burns 1971: 1, Williams and Kosztarab 1972: 164, Kosztarab 1977: 184, Gill 1982: 1, Hamon and Williams 1984: 119, Gill 1988: 111.

Specimens studied.—*Liriodendron tulipifera*: 1(4), Valley Mills, IN, H. Morrison (UCDC); 1(5), Knoxville, TN, let. 24 Sep 1941, G. M. Bentley (USNM); 1(2), Montgomery Co., Blacksburg, VA, 16 Sep 1968, MLW (AUEM); 1(10), Simpson, IL, 7 Aug 1969, J. E. Appleby (USNM); 1, Green Co., Mt. Morris, PA, 1 Apr 1970, D. P. Burns (FSCA). *Liriodendron*: 2(9), College Park, MD, 9 May 1938, H. S. McConnell (USNM); 1(11), San Jose, CA, 16 Nov 1945, let. E. O. Essig, Foster (USNM). Tulip poplar: 1(12), Kennett Sq., PA, 21 Aug 1950, C. A. Thomas (USNM). Tulip tree: 1(16), Kingston, NY, 10 Aug 1949, J. A. Naegele (USNM).

Additional host plants and distribution.—*Toumeyella liriodendri* probably is native to the North American yellow-poplar area ranging from New York and Connecticut to Florida and west through the Mississippi River Valley (Burns and Donley 1970). It also occurs in California on shade and ornamental plantings of yellow-poplar and magnolia (Williams and Kosztarab 1972).

Toumeyella liriodendri occurs on numerous hosts including: *Magnolia acuminata, M. grandiflora, M. nigra, M. obovata, M. sinensis, M. soulangiana, M. soulangiana* var. *alexandrina, M. stellata, M. virginiana, Michellia fuscata*, and cape jessamine (*Gardenia jasminoides*?). Numerous authors report varied hosts such as *Cephalanthus* spp., *Gardenia jasminoides, Gordonia lasianthus, Juglans* spp., *Tilia* spp. (Donley and Burns 1965), *Magnolia lenni* (Merrill 1953), *Magnolia kobus* (Sleesman 1945), *Ascyrum edinianum, A. hypericoides, A. tetrapetalum, Carya cordiformis, Cassia fasciculata*, and *Hypericum cistifolium* (Hamon and Williams 1984). It is doubtful that *T. liriodendri* occurs on *Cephalanthus* spp., but rather is a misidentification of *T. cerifera* (Williams and Kosztarab 1972). Records on *Ascyrum* spp. and *Hypericum* spp. are most likely misidentifications of an undescribed *Toumeyella* species.

General appearance.—Body (Fig. 3-A)

oval, 559 (506–724) long, 333 (293–521) wide. Dorsum.—Marginal setae (Fig. 3-B) 24 (19–31) long on head tapering to 10 (7–12) long near anal cleft, stout, tapering to a point, often curved posteriorly, distribution: 8 anteriorly between eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 3-C) in each spiracular furrow; median seta 29 (25–33) long, lateral setae 7 (6–8) long. Small (2 μm) bilocular (Fig. 3-D) and small (2 μm) quinquelocular (Fig. 3-E), occasionally 4- and 6-locular, pores in submedian and submarginal longitudinal rows. Anal plates (Fig. 3-H).—Each plate with dorsum densely reticulated, 66 (58–69) long, 32 (28–37) wide; cephalolateral margin 43 (37–47) long, caudolateral margin 36 (30–41) long. Venter.—Antennae (Fig. 3-L) 161 (150–171) long. Legs (Fig. 3-M) 238 (229–253) long, microctenidia (Fig. 3-N) at tibial apex; tarsal digitules (Fig. 3-O) 48 (42–52) and 34 (27–38) long; claw digitules (Fig. 3-P) 24 (22–25) long; claws (Fig. 3-Q) with denticle. Diagnosis.—*Toumeyella liriodendri* is most similar to *T. nectandrae*, though dorsal multilocular disc pores have only been observed in *T. liriodendri*. All other species have simple dorsal disc pores.

Toumeyella mirabilis (Cockerell)
Fig. 4

Lecanium mirabile Cockerell 1895: 3.
Toumeyella mirabilis (Cockerell). Cockerell 1902: 452, Fernald 1903: 179, Ferris 1919: 45, Ferris 1921: 91, MacGillivray 1921: 181, Steinweden 1929: 227, Williams and Kosztarab 1972: 158, Taber et al. 1975: 439, Ward et al. 1977: 100.

Specimens studied.—Mesquite twigs: 1(7), Nogales, AZ, 21 Apr 1940 (USNM). *Prosopis juliflora* var. *velutina*: 3(8), Tucson, AZ, 11 May 1950, M.E. Elve (UCDC). *Prosopis* sp.: 3(10), Galiuro Mts., AZ, 26 May 1897, Hubbard (USNM); 3, Cochise Co., AZ, 27 Jul 1969, M. Kosztarab (AUEM).

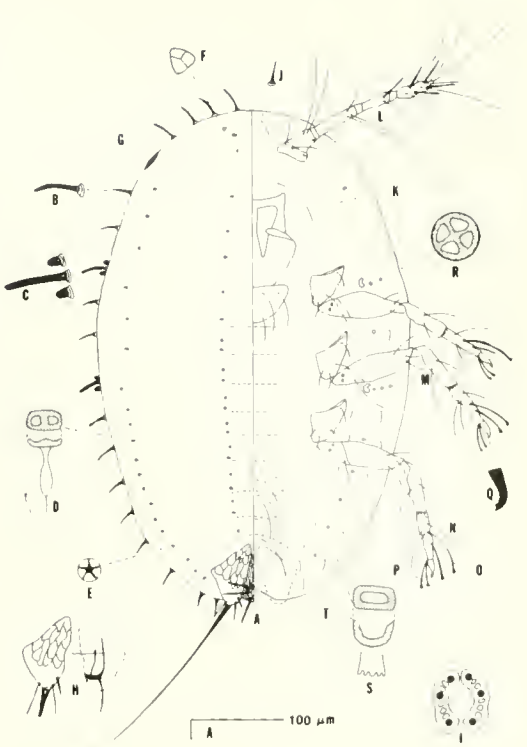

Fig. 3. First instar, *Toumeyella liriodendri* (Gmelin) 1789.

Additional host plants and distribution.—*Toumeyella mirabilis* has also been recorded on *Prosopis glandulosa* and *P. juliflora* var. *glandulosa*. *Toumeyella mirabilis* has been recorded from NM, TX and Mexico.

General appearance.—Body (Fig. 4-A) oval, 616 (514–847) long, 370 (319–503) wide. Dorsum.—Marginal setae (Fig. 4-B) 17 (11–27) long, stout, tapering to a point, curved posteriorly, distribution: 8 anteriorly between eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 4-C) in each spiracular furrow; median setae 78 (32–128) long: in anterior set, lateral setae 13 (10–20) long; in posterior set, anterior lateral seta 12 (7–17) long, and posterior lateral seta 21 (9–

Fig. 4. First instar, *Toumeyella mirabilis* (Cockerell) 1895.

33) long. Small (2 µm) bilocular pores (Fig. 4-D) in a submedian longitudinal row. Simple disc pores (Fig. 4-E) in submedian and submarginal longitudinal rows. Anal plates (Fig. 4-H).—Each plate with dorsum densely reticulated, 78 (72–84) long, 33 (25–38) wide; cephalolateral margin 48 (43–52) long, caudolateral margin 43 (35–48) long. Venter.—Antennae (Fig. 4-L) 170 (157–179) long. Legs (Fig. 4-M) 299 (267–323) long, microctenidia at tibial apex absent; tarsal digitules (Fig. 4-N) 58 (54–61) and 43 (38–46) long; claw digitules (Fig. 4-O) 28 (23–33) long; claws (Fig. 4-P) with denticle. Diagnosis.—The spiracular setae will serve to separate *T. mirabilis* from all other *Toumeyella*. In *T. mirabilis* the median spiracular setae are 5–6 times longer than the anterior set of laterals, small dorsal bilocular pores occur in submedian rows only, anal plates are densely reticulated, and microctenidia are absent. *Toumeyella mirabilis* has only been collected on *Prosopis*.

Toumeyella nectandrae Hempel
Fig. 5

Toumeyella nectandrae Hempel 1929: 64, Lepage 1938: 347.

Specimens studied.—*Nectandra* sp.: 3(24), Sao Roque, S. Paulo, Brazil, 27 Oct 1931, H. S. Lepage (AUEM).

General appearance.—Body (Fig. 5-A) oval, 490 (430–546) long, 282 (247–314) wide. Dorsum.—Marginal setae (Fig. 5-B) 30 (25–37) long, stout, slightly curved posteriorly, distribution: 8 anteriorly between eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 5-C) in each spiracular furrow; median setae 34 (31–38) long, lateral setae 8 (6–19) long. Small (2 µm) bilocular (Fig. 5-D) and simple disc (Fig. 5-E) pores in submedian and submarginal longitudinal rows. Anal plates (Fig. 5-H).—Each plate with dorsum densely reticulated, 61 (53–67) long, 30 (27–32) wide; cephalolateral margin 37 (28–41) long, caudolateral margin 38 (32–42) long. Venter.—Antennae (Fig. 5-K) 159 (152–165) long. Legs (Fig. 5-L) 231 (211–242) long, microctenidia (Fig. 5-M) at tibial apex; tarsal digitules (Fig. 5-N) 43 (41–46) and 30 (26–32) long; claw digitules (Fig. 5-O) 21 (20–22) long; claws (Fig. 5-P) with denticle. Diagnosis.—*Toumeyella nectandrae* is similar to *T. liriodendri*, but *Toumeyella nectandrae* has simple dorsal disc pores, whereas *T. liriodendri* has multilocular dorsal disc pores.

Toumeyella parvicornis (Cockerell)
Fig. 6

Lecanium parvicorne Cockerell 1897: 90.
Toumeyella parvicornis (Cockerell). Cockerell 1902: 452, Fernald 1903: 179, Wil-

son 1917: 59, Ferris 1920: 42, MacGillivray 1921: 181, Merrill and Chaffin 1923: 274, Williams and Kosztarab 1972: 171, Williams and Cobb 1982: 93, Hamon and Williams 1984: 122.

Lecanium (Toumeyella) numismaticum Pettit and McDaniel 1920: 8.

Toumeyella numismaticum Pettit and McDaniel. Steinweden 1929: 227, Craighead and Middleton 1930: 17, Orr and Hall 1931: 1087, Felt and Rankin 1932: 390, Doane et al. 1936: 375, Dodge and Rickett 1943: 485, Sleesman 1945: 44, Craighead 1950: 144, Merrill 1953: 110, Rabkin and Lejeune 1954: 570, McIntyre 1960: 325, MacAloney 1961: 1, Smirnoff and Valero 1975: 236.

Specimens studied.—Long leaf pine: 1(10), Alachua Co., FL, 15 Mar 1954, G. Merrill (USNM). *Pinus* sp.: 1(8), Houston Co., AL, 16 Apr 1976, Reafield Vester (AUEM). *P. elliottii:* 1(6), Baldwin Co., Perdido, AL, 12 May 1978, Charles H. Ray (AUEM). *P. montana:* 1(15), Washington, D.C., 17 Jul 1947, Wester (USNM). *P. palustris:* 1(3), Miami, FL, 6 Sep 1977, CHR (AUEM). *P. rigida:* TYPE, 1(2), Lake City, FL, 10 Apr 1897, A. L. Quaintance (AUEM). *P. taeda:* 2(4), Auburn University Insectary, Auburn, AL, 24 Oct 1974, CHR (AUEM). *P. virginiana:* 1(4), Blount Co., nr. Oneonta, AL, 7 Aug 1981, CHR (AUEM). Spruce: 1(3), Mathews Co., VA, 31 May 1968, T. E. Dinwiddie (AUEM).

Additional host plants and distribution.—*Toumeyella parvicornis* occurs primarily on pine species including: *Pinus nigra, P. strobus* (Williams and Kosztarab 1972), *P. banksiana, P. caribaea, P. clausa, P. densiflora, P. echinata, P. glabra, P. heterophylla, P. inops, P. mugo, P. mugo* var. *pumilio, P. mugo* var. *rostrata, P. pinea, P. ponderosa, P. radiata, P. resinosa, P. sinensis, P. sylvestris,* and *Zygocactus truncatus.*

Toumeyella parvicornis has been recorded in most states east of the Mississippi River and north to Manitoba, Canada (Williams and Kosztarab 1972) as well as IA, NB, ND, SD, and WI (MacAloney 1961).

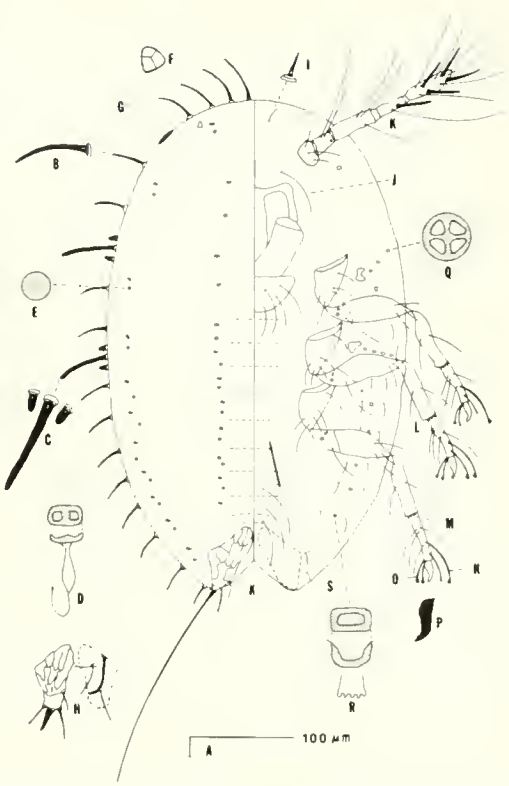

Fig. 5. First instar, *Toumeyella nectandrae* Hempel 1929.

General appearance.—Body (Fig 6-A) oval, 617 (487–902) long, 348 (284–561) wide. Dorsum.—Marginal setae (Fig. 6-B) 17 (12–21) long on head tapering to 13 (9–16) long near anal cleft, slender, curved posteriorly, distribution: 8 anteriorly between eyes, 3 on each side between eyes and anterior spiracular furrow, 3 on each side between anterior and posterior spiracular furrow, 16 on posterior of body. Two setae at apex of each spiracular furrow undifferentiated from marginal setae. Bilocular pore clusters (Fig. 6-C) in a submarginal longitudinal row. Simple disc pores (Fig. 6-D) in submedian and submarginal longitudinal rows. Anal plates (Fig. 6-G).—Each plate

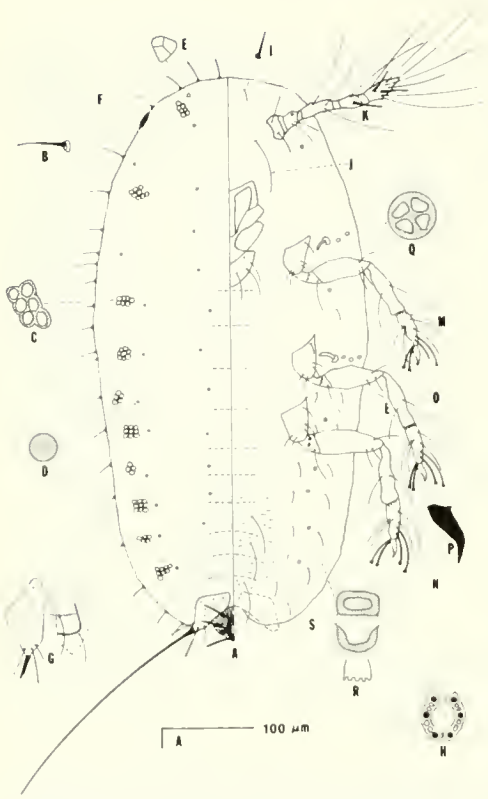

Fig. 6. First instar, *Toumeyella parvicornis* (Cockerell) 1897.

with sparsely distributed microspines on dorsum, 64 (56–70) long, 27 (25–31) wide; cephalolateral margin 36 (30–43) long, caudolateral margin 39 (36–43) long. Venter.—Antennae (Fig. 6-K) 183 (162–207) long. Legs (Fig. 6-L) 249 (231–271) long, microctenidia (Fig. 6-M) at tibial apex; tarsal digitules (Fig. 6-N) 49 (40–57) and 35 (30–39) long; claw digitules (Fig. 6-O) 24 (21–30) long; claws (Fig. 6-P) simple, without denticle. Diagnosis.—Dorsal bilocular pore clusters, spiracular setae undifferentiated from marginal setae, and simple tarsal claws are characteristics unique to *T. parvicornis*.

Toumeyella pini (King)
Fig. 7

Lecanium pini King 1901: 334.
Toumeyella (?) *pini* (King). Cockerell 1902: 452, Fernald 1903: 179.
Lecanium corrugatum Thro 1903: 216, Fernald 1903: 179.
Lecanium (*Toumeyella*) *corrugatum* (Thro). Pettit and McDaniel 1920: 6.
Toumeyella corrugatum (Thro). Harned 1923: 26, Doane et al. 1936: 375.
Toumeyella pini (King). Ferris 1920: 42, MacGillivray 1921: 181, Steinweden 1929: 227, Craighead and Middleton 1930: 17, Doane et al. 1936: 375, Dodge and Rickett 1943: 485, Craighead 1950: 145, MacAloney 1961: 3, Williams and Kosztarab 1972: 171, Hamon and Williams 1984: 124.

Specimens studied.—*Pinus mugo:* 1(2), Oxford, CT, let. of 13 Jul 1939, R. C. Brown (USNM); 1(9), Waynesboro, VA, 31 May 1941, F. R. Freund (USNM). *P. pungens:* 1(2), Blain, PA, 30 July 1959, A. T. Drooz (USNM). *P. taeda:* 1, Auburn, AL, 25 Jul 1974, CHR (AUEM); 1(4), Airport Marsh, Dauphin Island, Mobile Co., AL, 13 May 1978, CHR (AUEM); 1(2), Lee Co., Auburn, AL, 21 Jun 1977, CHR (AUEM). *P. virginiana:* 1(10), V.P.I. Plot 531/d, Blacksburg, VA, 11 May 1969, MLW (VPIC). Red pine: 1(10), Cole Nursery, Tazewell Co., VA, Jun 1957, F. R. Freund (USNM). Pine: 1(3), McConnelsburg area, PA, 10 June 1948, G. Sleesman (USNM).

Additional host plants and distribution.—*Toumeyella pini* has been reported on numerous pine species including: *Pinus contorta, P. resinosa, P. sylvestris* (Williams and Kosztarab 1972), *P. palustris, P. serotina* (Hamon and Williams 1984), *P. austriaca* (Jarvis and Guelph 1911), *P. divaricatus. P. echinata, P. elliottii, P. pinaster, P. rigida,* and *P. strobus.*

The type specimen was collected in NY with subsequent collections in TX (Hamon and Williams 1984), DC, FL, GA, MD, MI, MS, NJ, OH, and SC.

General appearance.—Body (Fig. 7-A) oval, 594 (441–921) long, 336 (264–494) wide. Dorsum.—Marginal setae (Fig. 7-B) 22 (14–32) long on head tapering to 12 (9–15) long near anal cleft, slender, curved posteriorly, distribution: 8 anteriorly between

eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 7-C) in each spiracular furrow; median setae 21 (19–25) long, lateral setae 7 (5–10) long. Small (2 μm) bilocular (Fig. 7-D) and simple disc (Fig. 7-E) pores in submedian and submarginal longitudinal rows. Anal plates (Fig. 7-H).—Each plate with sparsely distributed microspines on dorsum, 63 (57–73) long, 30 (23–35) wide; cephalolateral margin 38 (31–47) long, caudolateral margin 38 (31–47) long. Venter.—Antennae (Fig. 7-L) 166 (143–183) long. Legs (Fig. 7-M) 237 (219–261) long, microctenidia (Fig. 7-N) at tibial apex; tarsal digitules (Fig. 7-O) 49 (33–56) and 33 (27–36) long; claw digitules (Fig. 7-P) 21 (16–25) long; claws (Fig. 7-Q) with denticle. Biological notes.—*Toumeyella pini* is often found in mixed infestations with *T. parvicornis* (Williams and Kosztarab 1972). Diagnosis.—*Toumeyella pini* appears similar to *T. virginiana*. *Toumeyella pini* has small dorsal bilocular pores in submarginal and submedian longitudinal rows, whereas *T. virginiana* has bilocular pores in submarginal, submedian, and intermediate longitudinal rows.

Toumeyella quadrifasciata (Cockerell)
Fig. 8

Lecanium quadrifasciatum Cockerell 1895: 3.

Toumeyella quadrifasciata (Cockerell). Cockerell 1902: 452, Fernald 1903: 179, MacGillivray 1921: 181.

Specimens studied.—*Robinia neomexicana:* TYPE, 7(37), Organ Mts., NM, Ed Owen (AUEM).

General appearance.—Body (Fig. 8-A) oval, 579 (514–622) long, 324 (309–343) wide. Dorsum.—Marginal setae (Fig. 8-B) 22 (19–27) long on head tapering to 15 (12–18) long near anal cleft, slender, curved posteriorly, distribution: 8 anteriorly between eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 8-C) in each spiracular furrow; median setae 27 (25–32) long, lateral setae 8 (6–9) long. Large (4 μm) bilocular (Fig. 8-D) and simple disc (Fig. 8-E) pores in submedian and submarginal rows. Bilocular pores often bent in a bow-shaped configuration. Anal plates (Fig. 8-H).—Each plate with dorsum densely reticulated, 67 (63–70) long, 35 (31–37) wide; cephalolateral margin 44 (38–47) long, caudolateral margin 41 (40–44) long. Venter.—Antennae (Fig. 8-L) 169 (157–181) long. Legs (Fig. 8-M) 270 (261–279) long, microctenidia at tibial apex absent; tarsal digitules (Fig. 8-N) 47 and 32 long; claw digitules (Fig. 8-O) 24 (23–26) long; claws (Fig. 8-P) with denticle. Diagnosis.—Dorsal bilocular pores (>3 μm) which are predominantly bow shaped, in submarginal and submedian longitudinal rows occur only in *T. quadrifasciata*.

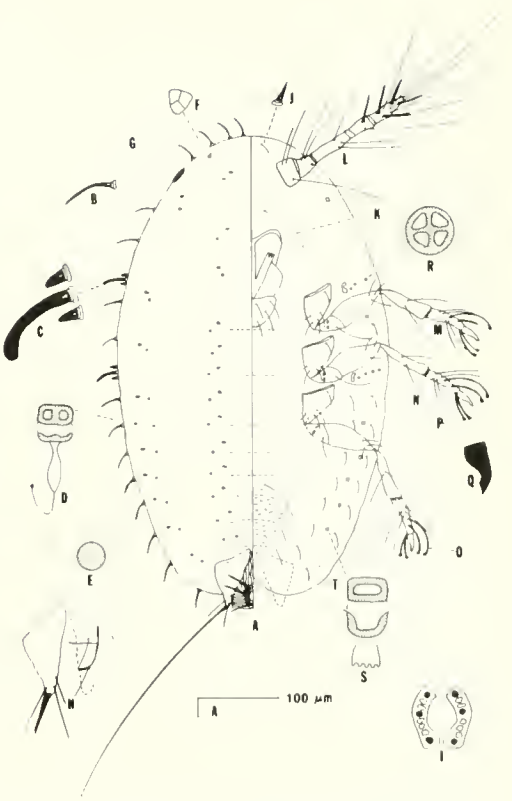

Fig. 7. First instar, *Toumeyella pini* (King) 1901.

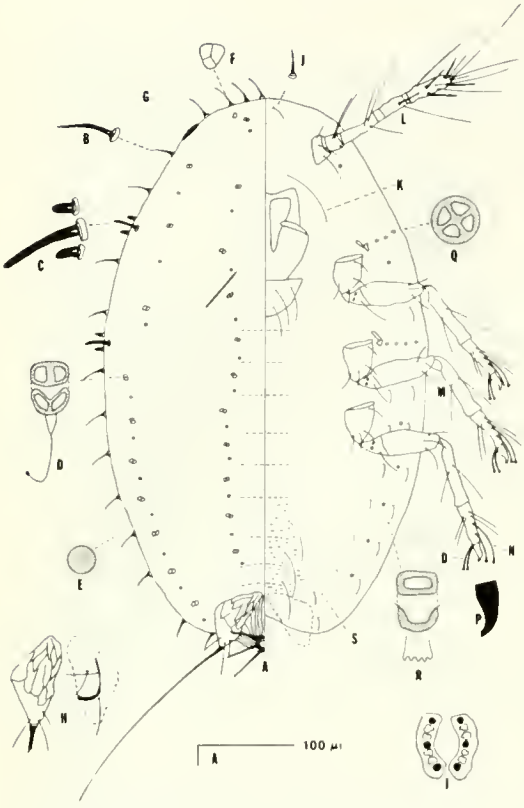

Fig. 8. First instar, *Toumeyella quadrifasciata* (Cockerell) 1895.

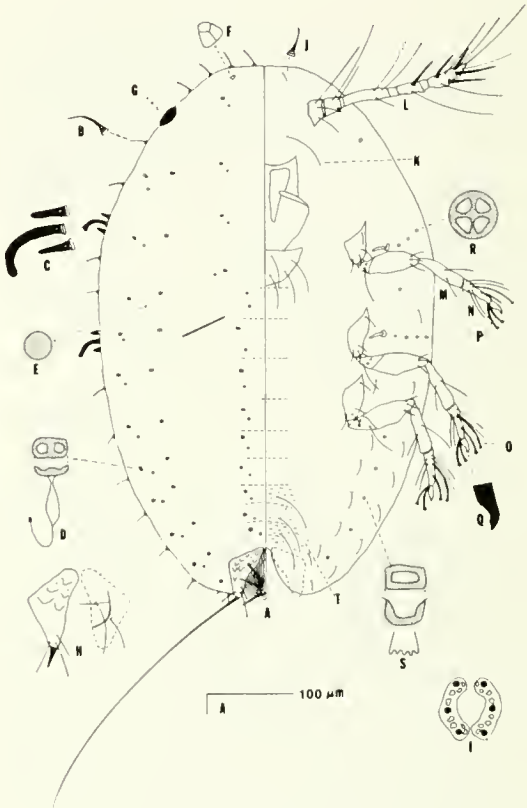

Fig. 9. First instar, *Toumeyella virginiana* Williams & Kosztarab 1972.

Toumeyella virginiana
Williams and Kosztarab
Fig. 9

Toumeyella virginiana Williams and Kosztarab 1972: 182, Hamon and Williams 1984: 126.

Specimens studied.—*Pinus:* 1(2), Auburn, AL, 26 Jun 1974, L. C. Ray (AUEM); 1(7), Pine Mt. Camp 35A, Harris Co., GA, 5 May 1979, K. Manuel (AUEM). *P. echinata:* 2(4), old water works road, Auburn, AL, 15 Aug 1974, MLW, J. Gilder, CHR (AUEM); 1(4), Bullock Co., Perote, AL, 26 Apr 1975, MLW (AUEM). *P. taeda:* 1(2), Dorchester Co., MD, 16 Sep 1971, MLW (AUEM); 2(4), Auburn, AL, 19 Jun 1974, L. C. Ray (AUEM); 1(2), Elmore Co., AL, 10 Aug 1974, CHR (AUEM).

Additional host plants and distribution.—*Toumeyella virginiana* has been collected on *Pinus elliottii, P. palustris,* and *P. virginiana.* Hamon and Williams (1984) report occurrence on *P. clausa* and *P. glabra.*

Toumeyella virginiana has been collected in FL and VA.

General appearance.—Body (Fig. 9-A) oval, 618 (330–965) long, 398 (318–681) wide. Dorsum.—Marginal setae (Fig. 9-B) 12 (10–16) long, slender, curved posteriorly, distribution: 8 anteriorly between eyes, 2 on each side between eyes and anterior spiracular setae, 2 on each side between anterior and posterior spiracular setae, 16 on posterior of body. Three spiracular setae (Fig. 9-C) in each spiracular furrow; median setae 20 (16–25) long, lateral setae 8 (5–12) long.

Small (2 μm) bilocular pores (Fig. 9-D) in submedian, submarginal and intermediate longitudinal rows. Simple disc pores (Fig. 9-E) in submedian and submarginal longitudinal rows. Anal plates (Fig. 9-H).—Each plate with dorsum coarsely reticulated; 73 (68–77) long, 34 (27–38) wide; cephalolateral margin 47 (38–52) long, caudolateral margin 45 (35–52) long. Venter.—Antennae (Fig. 9-L) 178 (152–196) long. Legs (Fig. 9-M) 232 (225–270) long, microctenidia (Fig. 9-N) at tibial apex; tarsal digitules (Fig. 9-O) 45 (36–51) and 29 (25–31) long; claw digitules (Fig. 9-P) 21 (19–25) long; claws (Fig. 9-Q) with denticle. Diagnosis.—*Toumeyella virginiana* appears quite similar to *T. pini* except for the presence of small dorsal bilocular pores in submedian, submarginal, and intermediate longitudinal rows. *Toumeyella pini* has dorsal bilocular pores in submedian and submarginal longitudinal rows only.

Discussion

The first-instar nymphs of all species of *Toumeyella* included in this study can be distinguished by morphological characters, but no means of distinguishing sexual dimorphism in the first instar were found. Also, no group characteristics were observed which would differentiate the *Pinus* feeding species of *Toumeyella* (*T. parvicornis, T. pini,* and *T. virginiana*) from those species associated with non-pine hosts (*T. cerifera, T. liriodendri, T. mirabilis, T. nectandrae,* and *T. quadrifasciata*).

The 8 first-instar *Toumeyella* described in this paper share many features with first instars of *Pseudophilippia quaintancii* Cockerell and *Neolecanium cornuparvum* Thro, most significantly 5-segmented antennae. Steinweden (1929) considered *Toumeyella, Neolecanium,* and *Pseudophilippia* as constituting one genus, while Williams and Kosztarab (1972) treated all three as valid genera. Comparison of *Toumeyella* first instars with descriptions of first instars of *Pseudophilippia quaintancii* and *Neolecanium cornuparvum* by Ray and Williams (1980, 1983) confirms the close relationship of the *Toumeyella* to these two genera and further justifies the placement of *Toumeyella, Neolecanium,* and *Pseudophilippia* in the tribe Toumeyellini. The invaginated bilocular pores of *P. quaintancii* are unique to that species and will separate it from all other Coccidae, but *N. cornuparvum* seems to fit well with *Toumeyella* based on comparisons of the first instar nymph and adult male. The dense pattern of bilocular pores of the adult female, however, suggests a closer relationship to other *Neolecanium* species. Preliminary investigations by the junior author indicate that some of the species currently placed in *Neolecanium* are actually closer to *Toumeyella* than other members of *Neolecanium.* Because of such confusion within the genus we feel it is premature to move *N. cornuparvum* from its current placement until a review of *Neolecanium* is conducted.

A ninth species, *T. sonorensis* (Cockerell and Parrott 1899), included in this study, has 6-segmented antennae and is not congeneric with the genotype, *T. mirabilis* or the remaining species studied, which have 5-segmented antennae. Preliminary investigations of the adult female morphology seem to indicate that *T. sonorensis* should be in a different genus than *Toumeyella,* but further revisionary work is needed before determining the placement of this species historically included in the *Toumeyella.* Additionally, distribution gaps within the United States and among temperate, neotropical, and tropical regions suggest further collecting in these areas is needed.

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UNUSUAL CADDISFLY (TRICHOPTERA) FAUNA OF SCHOOLHOUSE SPRINGS, LOUISIANA, WITH DESCRIPTION OF A NEW SPECIES OF *DIPLECTRONA* (HYDROPSYCHIDAE)

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Abstract.—The caddisflies (Trichoptera) of Schoolhouse Springs, Jackson Parish, Louisiana, have been studied since 1959, first by H. H. Ross and some of his colleagues and subsequently by several of his students. At least 43 species of caddisflies have been captured in or beside the spring, one of which (belonging to the genus *Diplectrona*, Hydropsychidae) is described in this paper. The Springs are the type locality for five caddisfly species and one stonefly species. Five of these species of insects are known from nowhere else. *Lepidostoma serratum* Flint and Wiggins occurs here apparently as an isolated population, far removed from populations in Connecticut and North Carolina.

Key Words: Trichoptera, spring faunas, Louisiana, *Diplectrona*

Trichoptera and other aquatic insects have been studied sporadically at Schoolhouse Springs, Jackson Parish, Louisiana (T17N, R1W, about middle of Sec. 12, about 6 miles north of Eros), at least since 1959 by H. H. Ross and several of his colleagues and students. The fauna and flora of the Springs are sufficiently unusual that the Louisiana Nature Conservancy recently purchased the site to help assure perpetual protection for it and its biota.

Schoolhouse Springs are located about a mile west of the community of Indian Village, named for the band of Choctaws which inhabited the area until the 1820's. The Springs were named by Ross in 1973 for Springhill Academy which once stood above them on the hill about 100-200 m east (Brown and Asken 1982). For years the site was relatively unknown and undisturbed except by aquatic entomologists. However, in 1987 the land surrounding the Springs was sold and slated for logging and development. When the authors urged protection of the area because of its unique aquatic biota, the Louisiana Nature Conservancy immediately launched a thorough investigation and named the Springs a high priority site for acquisition. In September 1988, 30 acres, including the Springs and a portion of the bayhead community along the springbrook, were purchased and designated as a preserve by the Conservancy.

At least five distinct, permanent, small springs of cool, clear water bubble from white sands at the base of moderately steep slopes and converge to form Schoolhouse Branch, a shallow stream averaging less than 10 cm depth. Vegetation surrounding the Springs is primarily a mixed hardwood-pine forest; however, a bayhead swamp community is supported in thick accumulations of peaty muck surrounding the springhead and along Schoolhouse Branch.

At least 43 species of Trichoptera have been recognized from Schoolhouse Springs (Table 1), including three endemics: *Cheumatopsyche morsei* Gordon, 1974; *Hydroptila ouachita* Holzenthal and Kelley, 1983; and *Chimarra holzenthali* Lago and Harris, 1987. Herein, JCM adds a fourth endemic caddisfly species, belonging to the genus *Diplectrona*. The stonefly *Leuctra szczytkoi* Stark and Stewart, 1981 (Plecoptera, Leuctridae) apparently is endemic to the Springs, also. In addition, Schoolhouse Springs is the type locality for *Agarodes libalis* Ross and Scott, 1974.

The range of the sister species of each of the endemic caddisflies lies to the east or north of Schoolhouse Springs. The sister species of the new *Diplectrona* species is *D. modesta* Banks, whose range includes eastern North America from Florida to New Hampshire and Quebec to Illinois to western Arkansas, northern Louisiana (Schoolhouse Springs), and southern Mississippi. The sister species of *C. holzenthali* is *Chimarra feria* Ross (Lago and Harris 1987), a species whose range includes eastern Texas, northwestern Louisiana, the Ouachita and Ozark Mountains, and the Great Lakes region. Speaking of *C. holzenthali* Ross (1965) noted that "it is possible that [this] local endemic species originated from windblown vagrants. It is also possible that during the glacial maxima some of the connecting streams from the Ouachita Mountains were cool enough to afford avenues of dispersal by which caddisflies reached their present spring habitats." The sister species of *C. morsei* is *Cheumatopsyche virginica* Denning (Gordon 1974), from Coastal Plain localities in New Jersey, Delaware, Virginia, South Carolina, Georgia, Florida, and southern Mississippi (Gordon 1974, Morse et al. 1980, Harris et al. 1982, Lago et al. 1982, Lake 1984). That of *H. ouachita* is *Hydroptila poirrieri* Holzenthal and Kelley, from Mississippi and southeastern Louisiana (Holzenthal and Kelley 1983). Thus it appears likely that the endemic species of Schoolhouse Springs evolved in isolation here after having arrived either as extensions of ranges of their ancestors from the North during Pleistocene glaciation (*D. rossi* and *C. holzenthali*) or as relict populations near the edge of the Mississippi Embayment and southeastern Coastal Plain (*C. morsei* and *H. ouachita*).

Showing a pattern similar to the latter two species, although yet without allopatric speciation, *Agarodes libalis* occurs throughout the southern Coastal Plain from Delaware to Florida to Louisiana; Schoolhouse Springs, its type locality, is at the western edge of its range (Ross and Scott 1974, McEwan 1980, Holzenthal et al. 1982, Lake 1984).

Lepidostoma (*Mormomyia*) *serratum* Flint and Wiggins apparently is the only species of this large genus occurring in the Springs. According to Weaver (1983, 1988), the only other populations known for the species are found in Connecticut and North Carolina. Collections of adults were made from 30 March through 19 May in the Springs; three prepupae taken on 24 August suggest that a second generation may appear here in the autumn.

Diplectrona rossi Morse
NEW SPECIES

Mature Larva: Length 9.0–15.0 mm; head capsule width 1.08–1.33 mm. Similar to *D. modesta* in general structure. Head (Fig. 1) generally dark brown to near black with three conspicuous reddish yellow regions on frontoclypeus, including pair of regions in its lateral broadened areas and single region at its dorsal apex, variably light brown regions in center and anterior margin of frontoclypeus not as conspicuous. Occipital region and dorsolateral areas light brown. Frontoclypeus evenly convex anteriorly, broadened laterally at mid-length to level of eyes, and with pair of variably obtuse angles near anterior tentorial pits. Mandibles resembling those of *D. modesta*, left mandible without high thumb-like dorso-

Table 1. Adult Trichoptera of Schoolhouse Springs, Louisiana. * = Species for which the type locality is Schoolhouse Springs.

Hydropsychidae		
Cheumatopsyche	*burksi* Ross	3 Jun–14 Sep
	**morsei* Gordon	27 May–3 Jun
	pasella Ross	3 Jun
	pettiti (Banks)	30 Mar–24 Aug
Diplectrona	*modesta* Banks	14 Apr–24 Aug
	**rossi* Morse, n. sp.	14 Apr–7 Jul
Hydropsyche	*decalda* Ross	14 Apr
	orris Ross	8 May–24 Aug
	prob. *placoda* Ross	3 Jun
Potamyia	*flava* (Hagen)	7 Jul
Hydroptilidae		
Hydroptila	*novicola* Blickle & Morse	14 Apr
	remita Blickle & Morse	3 Jun–24 Aug
	**ouachita* Holzenthal & Kelley	30 Mar–24 Aug
	waubesiana Betten	3 Jun–24 Aug
	spp. nr. *consimilis* Morton	7 Jul
	sp. *maculata* (Banks) Group	3 Jun
Orthotrichia	*aegerfasciella* (Chambers)	3 Jun–24 Aug
Oxyethira	*novasota* Ross	14 Apr–24 Aug
Lepidostomatidae		
Lepidostoma	*serratum* Flint & Wiggins	30 Mar–19 May
Leptoceridae		
Ceraclea	*cancellata* (Betten)	3 Jun
	protonepha Morse & Ross	14 Apr
	spongillovorax Resh	3 Jun
	transversa (Hagen)	14 Apr
Leptocerus	*americanus* (Banks)	8 May–7 Jul
Oecetis	*cinerascens* (Hagen)	14 Apr–24 Aug
	ditissa Ross	14 Apr
	inconspicua (Walker)	14 Apr–24 Aug
	nocturna Ross	8 May–3 Jun
	ochracea (Curtis)	24 Aug
	osteni Milne	14 Apr–27 May
Triaenodes	*ignitus* (Walker)	14 Apr–24 Aug
Limnephilidae		
Pycnopsyche	spp.	(larvae only)
Molannidae		
Molanna	*blenda* Sibley	14 Apr–8 May
	tryphena Betten	23–28 Apr—pupae
Philopotamidae		
Chimarra	*aterrima* Hagen	8 May–24 Aug
	**holzenthali* Lago & Harris	7 Jul–14 Sep
Polycentropodidae		
Neureclipsis	sp.	3 Jun
Nyctiophylax	*affinis* (Banks)	8 May–3 Jun
Polycentropus	*crassicornis* Walker	30 Mar
Phylocentropus	*lucidus* (Hagen)	24 Aug
	placidus (Banks)	30 Mar
Psychomyiidae		
Lype	*diversa* (Banks)	30 Mar–24 Aug
Sericostomatidae		
Agarodes	**libalis* Ross & Scott	19 May–7 Jul

lateral projection. [Left mandible of *D. modesta* with dorso-mesal brush of setae present but not illustrated by Ross 1944, fig. 286.]

Pupa: Length 9.0 mm. Similar to *D. modesta* in general structure. Left mandible with five teeth, basal tooth as far from others as next most basal tooth is from apex; right mandible with four teeth. Mesal fork of each apical process 1.5× as long as lateral fork.

Male: Length 8.8–9.5 mm; forewing 7.6–7.9 mm. Similar to male of *D. modesta* in general structure. Warts and other structures on dorsum of head (Fig. 3) similar in size and shape to those of male of *D. modesta* (Fig. 4), except with diagonal lines of posterior vertex behind pair of conical protuberances ending on epicranial stem (ep.su.), anteriad of transverse postoccipital sulcus (po.oc.). Antennae each with scape and pedicel usually at least as dark as, or darker than, flagellum. Eyes not unusually large; in dorsal view, ratio of greatest width of one eye to narrowest width of vertex (eye : vertex ratio) about 0.475; malar space (Fig. 5) slightly broader than for male of *D. modesta* (Fig. 6). Extreme lateral corners of pronotum, laterad of lateral warts, each with generally conspicuous pale cream-colored spot (Fig. 5, spt).

Male genitalia (Figs. 7–10): Similar to those of *D. modesta* in general structure. Anterolateral corners of sternum V each with long slender glandular structure. Tergum IX divided anteriorly (Fig. 8, IX), with pair of rugose patches. Superior appendages not distinct, represented by region of setae on pair of dorsolateral lobes (do.lat., = terga IX–X?), each lobe with apex truncate in lateral view (Fig. 7), acute dorsally. Tergum X divided longitudinally on meson, each half tapered in dorsal view (Fig. 8, X), rounded in lateral view (Fig. 7, X), lightly sclerotized and setose apically. Inferior appendages each with basal segment bent slightly caudad near apex in lateral view (Fig. 7, inf.app.), curved mesad and clavate in caudal view (Fig. 9), apical segment curved mesad and spatulate in caudal view. Phallus simple (Fig. 10), similar to that of *D. modesta*.

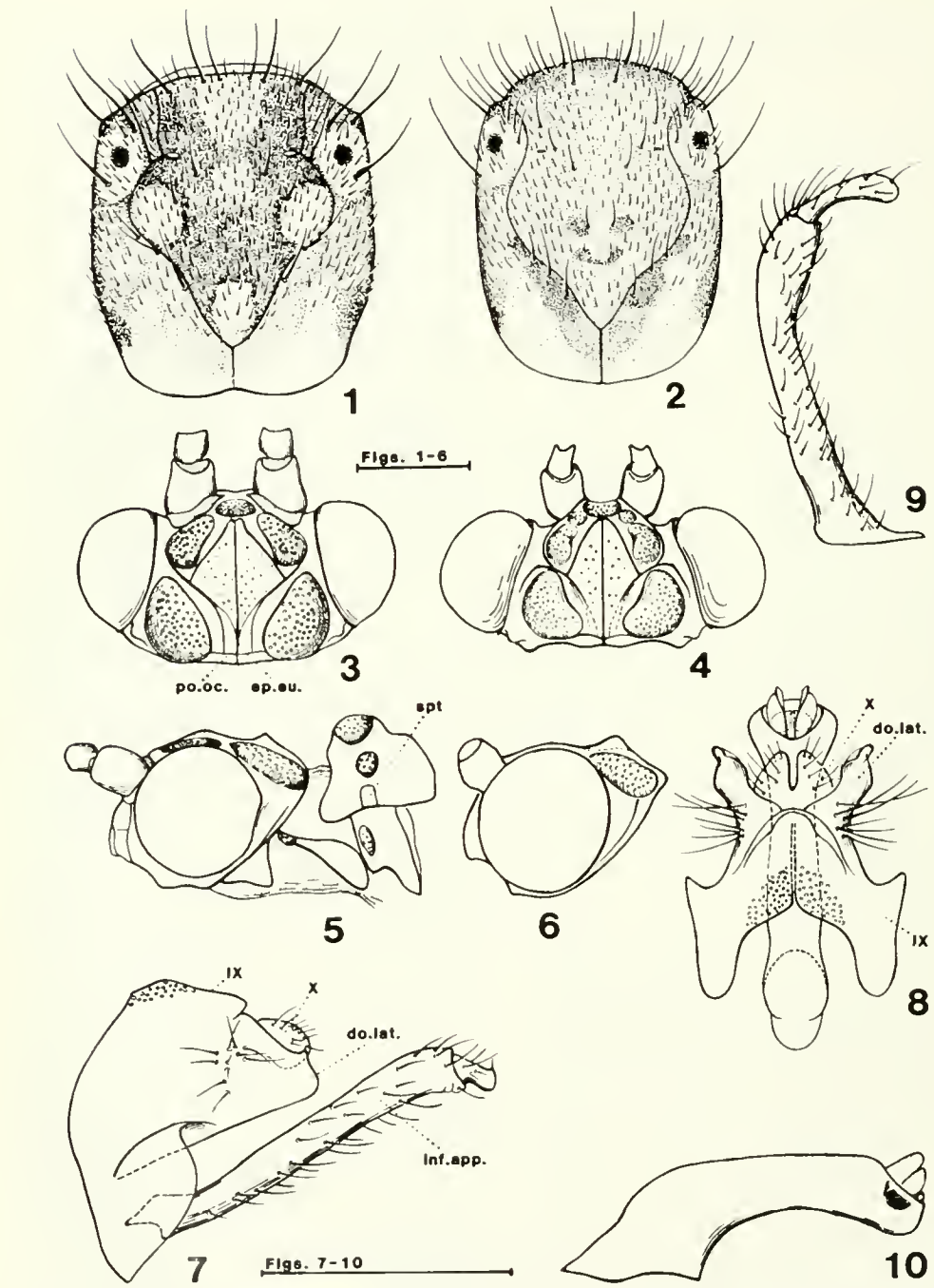
Female: Length 9.4–11.1 mm, forewing 8.0–9.2 mm. Similar to female of *D. modesta* in general structure. Warts and other structures on dorsum of head (Fig. 11) similar in size and shape to those of female of *D. modesta*, except with diagonal lines of posterior vertex behind pair of conical protuberances ending on epicranial stem, anteriad of transverse postoccipital sulcus. Eyes not unusually large. Extreme lateral corners of pronotum, laterad of lateral warts, without conspicuous pale cream-colored spots.

Female genitalia: Generally resembling those of *D. modesta* very closely. Median plate (Figs. 12–13) spatulate anteriorly, without longitudinal dorsal carina.

Holotype: Male, LOUISIANA: Jackson Parish; Schoolhouse Springs; R1W, T17N, Sec. 12; 6 miles north of Eros; 14 April 1988, mercury vapor and ultraviolet lights, C. B. Barr. Deposited in U.S. National Museum of Natural History (USNM).

Paratypes: All same locality: Same data as holotype, 1 male, 3 females, deposited in Louisiana State University Insect Collection (LSUC); 7 May 1987, C. B. and J. E. Barr, 4 females (USNM and LSUC); 27 May 1972, at light, Ross and Smith, 5 females, deposited in Clemson University Arthropod Collection (CUAC); 3 June 1973, J. C. Morse and J. A. Louton, 1 male, 1 female (CUAC); 30 March 1973, H. H. Ross et al., 26 larvae, 1 female pupa (CUAC); 14 April 1988, C. B Barr, 12 larvae, 1 prepupa (LSUC); 23 April 1982, R. W Holzenthal and S. W. Hamilton, 4 larvae (USNM); 28 April 1973, J. C. Morse, C. E Dunn, and J. A. Louton, 5 larvae (CUAC); 8 May 1987, C. B. Barr, 2 larvae (LSUC); 7 July 1973, J. C. Morse and J. A. Louton, 4 larvae (USNM).

Etymology: named for Dr. Herbert H. Ross, founder of modern trichopterology in North America, discoverer of the unusual aquatic insect fauna of Schoolhouse Springs and author of their name, and naturalist



Figs. 1–10. Characters of *Diplectrona rossi* and *D. modesta* larvae and males. 1, *D. rossi* larval head, dorsal view; 2, *D. modesta* larval head, dorsal view; 3, *D. rossi* male head, dorsal view; 4, *D. modesta* male head, dorsal view; 5, *D. rossi* male head and prothorax, left lateral view; 6, *D. modesta* male head, left lateral view; 7, *D. rossi* male genitalia, left lateral view; 8, *D. rossi* terga IX and X and phallus, dorsal view; 9, *D. rossi* left inferior appendage, caudal view; 10, *D. rossi* phallus, left lateral view. do.lat. = dorsolateral lobe of male genitalia (paired), ep.su. = epicranial suture, inf.app. = male inferior appendage (paired), IX = abdominal segment IX, po.oc. = postoccipital sulcus, X = abdominal segment X. Scale lines each 0.5 mm.

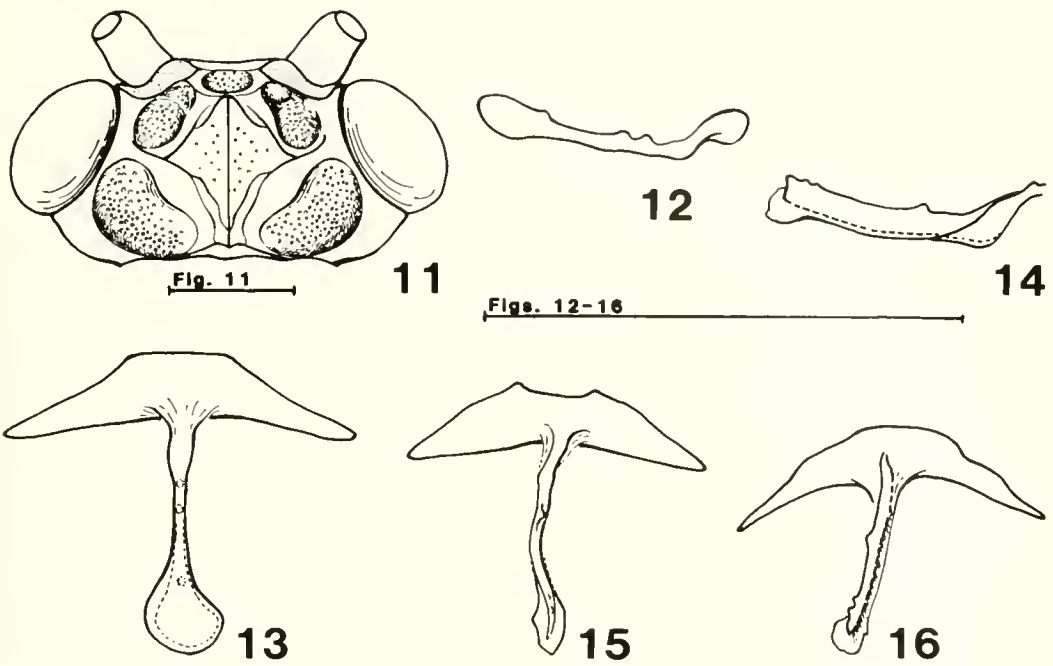


Fig. 11–16. Characters of *Diplectrona rossi* and *D. modesta* females. 11, *D. rossi* head, dorsal; 12, *D. rossi* median plate of genitalia, left lateral view; 13, *D. rossi* median plate of genitalia, dorsal view; 14, *D. modesta* median plate of genitalia, left lateral view; 15, *D. modesta* median plate of genitalia, dorsal view; 16, same, variation. Scale lines each 0.5 mm.

who first brought the senior author's attention to this species.

Diagnosis: Larvae of this species are readily distinguishable from those of *D. metaqui* in that the frons is evenly convex apically (versus notched, cf. Ross 1944, fig. 338, "Genus A") and the left mandible does not have a high thumb-like process (versus with this process, cf. Ross 1944, fig. 282, "Genus A"). The head is relatively broader than that of *D. modesta* (Fig. 2), but relatively narrower than that of *D. metaqui* (Ross 1944, fig. 338). Unlike both *D. metaqui* and *D. modesta*, the frons has a pair of variably obtuse angles near the anterior tentorial pits (Fig. 1; versus evenly curved, Fig. 2), and three conspicuous reddish yellow regions occur laterally and posteriorly on the frontoclypeus, sometimes visible even in the field. The larva of *D. californica* Banks, 1914, is unknown.

The pupa of this species differs from that of *D. modesta* in that the left mandible has five teeth (four in *D. modesta*, cf. Ross 1944, fig. 316), with the basal tooth as far from others as the next most basal tooth is from the apex; the right mandible has four teeth (five in *D. modesta*); and the mesal fork of each apical process is 1.5 × as long as the lateral fork (subequal in *D. modesta*, cf. Ross 1944, fig. 310A). The pupae of *D. californica* and *metaqui* have not been described.

Males of this species resemble those of *D. modesta* in the relative size of warts on the vertex and in the antennae with flagellum lighter than scape and pedicel (middle wart slightly smaller [Ross 1970, fig. 4B] and scape and pedicel lighter than flagellum in *D. metaqui*). The eyes of *D. rossi* are slightly smaller than those of *D. modesta* (eye : vertex ratio of *D. modesta* between 0.55 and 0.65) and clearly larger than those of *D. metaqui* (e:v = 0.39–0.40). *Diplectrona rossi* differs from both *D. modesta* and *D. metaqui* in having the diagonal lines of the posterior vertex (behind the pair of conical pro-

tuberances) ending on the epicranial stem, anteriad of the transverse postoccipital sulcus (Fig. 3; ending on the postoccipital sulcus in the other two species, Fig. 4). The genitalia of the male of this species differ from those of *D. modesta* and *D. metaqui* in the more nearly truncate apex of each dorsolateral lobe (Fig. 7; cf. Ross 1944, fig. 339). Also, in many specimens of *D. modesta,* the inferior appendage is nearly straight apically in lateral view, but curved posteriad in the three male specimens seen of this species (Fig. 7). The male genitalia of *D. metaqui, modesta,* and *rossi* all differ from those of *californica* in the pair of dorsolateral lobes distinct from the more mesal lobes of tergum X, not clearly separated in *californica* (Denning, 1965, as *D. margarita*; Flint 1966).

Females of this species differ from those of both *D. modesta* and *D. metaqui* in the same characters of the head mentioned for the males. Additionally, the pronotum of females of the type series all lack the conspicuous pale, cream-colored spot on the extreme lateral corners, laterad of the lateral warts, present in males of all three species (Fig. 5) and usually in females of *D. modesta.* The median plate of the genitalia (Figs. 12 and 13) lacks a longitudinal carina present on the median plate of *D. modesta* (Figs. 14–16). Characters of the pronotum and median plate of females of *D. californica* and *metaqui* are unknown.

Further comments: Associations of larvae and pupae with adults of this new species are circumstantial. All these life history stages differ from those of known species and occur uniquely in Schoolhouse Springs.

Two larvae of a *Diplectrona* species have been collected in a spring-fed stream in north-central Tennessee by D. Gillis and T. Kollers, students of Dr. S. W. Hamilton. These larvae resemble those of *D. rossi* in the presence of conspicuous light-colored spots on the frons and obtuse angles near the anterior tentorial pits. However, the background color of the head of these specimens is lighter than for *D. rossi,* the lateral spots on the frons are much larger, and a median spot is much more conspicuous than the posterior spot. A fifth North American species of this genus is suspected, but should be confirmed with data from other life history stages.

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MATING BEHAVIOR OF *ACIURINA MEXICANA* (ACZÉL) (DIPTERA: TEPHRITIDAE)

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Abstract.—Observations on the mating behavior of *Aciurina mexicana* (Aczél) in the laboratory are presented. Courtship and agonistic displays are named and described in detail. These displays include stereotypic body postures and wing movements, nuptial feeding, and abdominal inflation with odor production by males. Preliminary observations suggest that the male's nuptial gift is produced from the crop, and the source of the male odor is the abdominal pleura. Mating behavior of *A. mexicana* is compared with other *Aciurina* species and tephritid flies generally. Potential use of mating behavior in fruit fly systematics is noted.

Key Words: Tephritidae, *Aciurina*, mating behavior, sexual displays, nuptial gift, pheromone, systematics

At least 12 species of *Aciurina* occur in the western United States and northern Mexico (Steyskal 1984, Dodson and George 1986). Larvae of the species for which host plants are known form galls on asteraceous plants, primarily *Chrysothamnus* species (Steyskal 1984, Dodson 1987b).

Mating behavior has been observed for a number of *Aciurina* species. Tauber and Tauber (1967) reported the reproductive behavior and biology of *Aciurina ferruginea* (Doane) from California. Wangberg (1981) commented on the mating behavior of *A. ferruginea*, *A. maculata* (Cole), *A. semilucida* (Bates), *A. trixa* Curran, and an undescribed species (probably *A. idahoensis* Steyskal—see Steyskal [1984]) from Idaho. Dodson (1987b) described the mating behavior of *A. trixa* in New Mexico.

Dodson (1987b) predicted that most species of *Aciurina* would exhibit a similar mating strategy which he termed the "male-searching mating system." In this system, males move about the host plant scanning for conspecifics and attempt to copulate with any females encountered. Evidently, courtship is limited to a few brief wing displays and may not precede attempts at copulation. Successful mating is dependent more on a male's ability to maintain a mounted position on a female (Dodson pers. comm.).

Aciurina mexicana (Aczél) occurs in southern Arizona, southern California, and northern Mexico where larvae form stem galls on *Baccharis sarothroides* Gray (Steyskal 1984). Contrary to what has been reported for other *Aciurina* species, precopulatory behavior in *A. mexicana* is protracted and involves a number of complex sexual displays. This paper describes the mating behavior of *A. mexicana*.

MATERIALS AND METHODS

Specimens used in this study were swept from *B. sarothroides* located 14.3 km SE of Continental, Ariz. (Pima Co.) on 16 Feb.

and 1 Mar. 1986. Flies were separated by sex and caged, one to several, in 0.3–1 clear plastic cups. Cages were fitted with a cotton wick for water and ventilated by a series of small punctures around the top and bottom. Flies were fed a diet of honey containing a small quantity of nutritional yeast. The honey/yeast mixture was provided *ad lib* on a paper strip suspended in the cage; water was supplied twice daily by saturating the cotton wick. Flies were kept in the laboratory at ambient temperature, relative humidity, and photoperiod.

Observations of mating behavior began by placing a pair of flies in a 100 × 15 mm plastic petri dish. Trial length varied with the flies' activities. Trials were discontinued when one or both flies became unresponsive or agonistic. When copulation occurred, the pair was observed at least until they uncoupled. Petri dishes were changed between trials. Observations were made between 1025 and 1627 hours (MST) on nine dates between 25 Feb. and 10 Mar. 1986. Duration of mating activities was recorded to the nearest minute. Video recordings were used to help analyze behaviors.

Results

Courtship and agonistic displays.—Several displays were typical of one or both sexes of *A. mexicana* during courtship and agonistic interactions. To facilitate discussion, these displays are named and described below. Rotation of the wing refers to twisting the wing so its ventral surface is brought into an anteriorly directed position and the costal margin is pointing upward (Fig. 1). Rotating the wing 90° results in the wing blade being more or less perpendicular to the substrate. Angular measurements of wing movements are visual approximations.

Slow signal: One wing is brought slowly forward to an angle of ca. 90° to the long axis of the body (Fig. 2). As the wing is moved forward the wing blade is rotated ca. 90°. The forward movement of the wing may be smooth or by intermittent jerks accompanied by slight rotational adjustments. The wing is then slowly returned to its original position and the other wing brought forward in a similar manner. Both sexes exhibited this display.

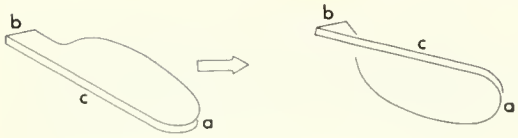
Wing fanning: Both wings are held outstretched at an angle of ca. 45° to the long axis of the body, with the wing blades rotated between ca. 45° and 90° (Fig. 3). Both wings are then brought forward and returned in short, very rapid, coupled strokes. Bouts of wing fanning were brief (ca. 1 s or less) and sometimes occurred in rapid succession. Only males exhibited this behavior.

Wing flicking: Both wings are held outstretched at an angle of ca. 45° to the long axis of the body, with the wing blades rotated ca. 90° (Fig. 4). Both wings are then brought forward and returned in short, quick strokes, with a brief pause between strokes. Only courting males used this display.

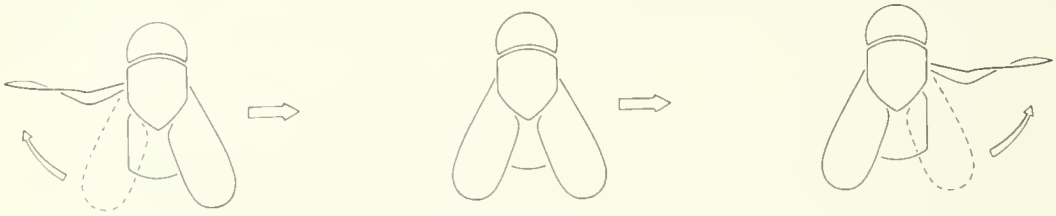
Wing thrust: Both wings are simultaneously and quickly brought forward to an angle of ca. 90° to the long axis of the body; wings are rotated ca. 90° as they are brought forward (Fig. 5). Wings are held in this position as the fly charges toward an intruder. Wing thrusts may be accompanied by waving the forelegs in an aggressive manner ("sparring"), with or without making contact. Wing thrusts and sparring were observed for both sexes.

Wing waving: Wings are alternately brought forward to an angle of ca. 90° to the long axis of the body; the wing is rotated ca. 90° as it is brought forward (Fig. 6). Each wing is returned to its initial position over the back of the fly as the other wing is brought forward. Wing waving is similar to the slow signal, but the wings are brought forward and returned in rapid succession. Wing waving was the basic component of female courtship.

Abdominal inflation: The abdominal pleura of males become swollen during courtship and agonistic intrasexual dis-

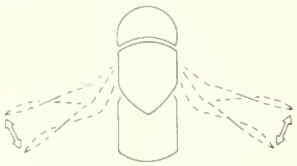


1



slow signal

2

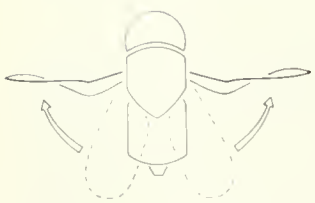


wing fanning

3

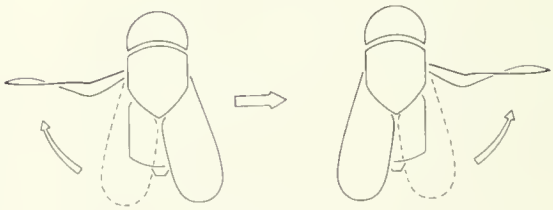
wing flicking

4



wing thrust

5



wing waving

6

Figs. 1–6. 1. Wing rotation in *Aciurina mexicana* (left anterolateral view). The wing blade goes from parallel to the substrate to perpendicular to the substrate (rotation = 90°). a, wing apex; b, wing base; c, costal margin. Figs. 2–6. Wing displays in *Aciurina mexicana* (dorsal view). 2, Slow signal. 3, Wing fanning. 4, Wing flicking. 5, Wing thrust. 6, Wing waving. See text.

plays. Inflation of the pleura is accompanied by the release of an odor, presumably a pheromone, that is easily detectable by humans.

Nuptial gift: During courtship males produce a clear fluid from their mouthparts and dab it onto the substrate with their labellum. Females are attracted to and feed on the fluid while males attempt mounting. The fluid becomes sticky as it dries. Nuptial gifts that were not entirely consumed were readily eaten by both sexes.

Mating behavior.—A total of 33 trials were conducted and 20.9 h of observations recorded. Courtship displays were observed for either one or both sexes during 26 trials: only males displayed in 11 trials, only females displayed in two trials, and both sexes displayed during 13 trials. No courtship was observed during seven trials. Copulation (n = 7) occurred only in trials where both sexes exhibited courtship displays. Males initiated courtship in 19 trials with two of these resulting in copulation; females initiated in three trials, one resulted in copulation; both flies began courting simultaneously during four trials, all resulted in copulation. Trials in which courtship did not lead to copulation (n = 19) were discontinued when one or both flies were unresponsive (n = 5) or agonistic (n = 14).

After being placed in a petri dish, flies walked about randomly, often with their wings outstretched, or groomed until one or both became cognizant of the other. Both sexes rhythmically extended and retracted their mouth parts during mating as well as nonmating activities. Courtship and mating were not limited to a particular surface within the dish.

The most typical and complete sequence of mating behaviors from courtship through copulation is given below. Deviations from this pattern are then discussed.

The body of males during noncourtship activities was held close to the substrate. During courtship, however, males extended their legs and held their bodies well above the substrate. In this raised posture males rocked from side to side and displayed wing flicking and abdominal inflation (n = 24). While displaying, males remained stationary or moved forward by short, uncoupled steps. Males typically approached females from the front. When within a few centimeters of the female, the male turned, moved a short distance away, turned back to face the female, and reapproached. This sequence was repeated several times prior to producing a nuptial gift.

Females responded to courting males by wing waving (n = 13). The intensity of wing waving was affected by the male's proximity. As the male moved away from the female, wing waving was less vigorous or ceased; as he reapproached, wing waving became more vigorous or was resumed.

After a period of reciprocal displays, the male, while continuing to display, became stationary and produced a nuptial gift (n = 7). Although males usually continued to court females that became unresponsive (n = 2) or agonistic (n = 4), nuptial gifts were produced only after vigorous wing waving by females. While continuing her wing waving, the female approached the male and began to feed on the nuptial gift. As the female fed, her wing waving became very rapid. Males displayed for a mean of 8.7 min (n = 7, median = 9 min, range = 2–17 min) before producing a nuptial gift. One male placed his gift on the side of the petri dish, three males placed their gifts on the dish bottom, and three placed a gift on the dish lid.

The male ceased displaying soon after the female began feeding on the nuptial gift. He then retreated a short distance and reapproached the female to attempt mounting. As the male moved away the female ceased to display but continued feeding. As he reapproached the female, his body was close to the substrate and his wings were folded tightly over his abdomen. Males usually

mounted from the side or rear by simply grabbing the female, or by pushing their head under one of the female's wings and climbing upon her abdomen. Females usually continued feeding and remained stationary while the male attempted to mount.

Males probed the tip of the female's oviscape with their surstyli after mounting. Prior to intromission the male grasped the female tightly by hooking his foretarsal claws over the anterolateral margin of her syntergum 1+2; his meso- and metatarsi remained on the substrate. The male maintained a grip on the female's syntergum after intromission; his mesotarsi were held loosely about her fifth or sixth tergum, and his metatarsi were held loosely about her oviscape or trailing behind, touching the substrate or not. The male's abdomen returned to its precourtship size after mounting.

After coupling (n = 7), a pair usually moved a short distance before becoming stationary and usually remained in one place if undisturbed. The male's wings were held over his abdomen during copulation; the female's wings were spread to accommodate his body. Copulation lasted a mean of 1.5 h (n = 6, range = 1.1–1.9 h). (Mean duration of copulation does not include one pair that became uncoupled when inadvertently disturbed.) Males remained motionless during copulation except for adjusting their posture when disturbed by intermittent grooming by the female. Females also were seen to slow signal during copulation.

Uncoupling was brief and seemingly without difficulty. Both sexes spent a short period grooming themselves after uncoupling. Males usually reinitiated courtship, but females either were unresponsive or actively rejected them. No male was seen to remount a female following copulation.

Several deviations from the pattern of courtship described above were observed. Males did not produce a nuptial gift in two of the seven trials that resulted in copulation. Duration of copulation for these two pairs was 1.4 and 1.5 h. During two trials where gifts were produced and the males were unsuccessful in their first attempts to mount, they reinitiated wing flicking and added more fluid to the gifts. One male added to the gift twice, the other six times; copulation followed in each case. In two other trials the female elicited and fed on a nuptial gift, but then vigorously evaded attempts by the male to mount. In four trials, males showing limited or no displays attempted to mount females; none of these resulted in copulation. During two trials females exhibited wing waving without previous courting by males. In one of these trials the male was unresponsive; in the other, the male attempted mounting and then exhibited agonistic behavior (wing thrusts) during the remainder of the trial (ca. 6 min).

Agonistic behavior.—Wing thrusts were used in an aggressive manner at close distances, inter- or intrasexually. Wing thrusts or sparring, or both, were often used by females to reject courting males (n = 11). Wing fanning accompanied by abdominal inflation and odor production was commonly observed between males in the same container. Wing fanning was observed between a male and female only once.

Females evaded a male's attempt to mount by simply walking or running away. While moving away, females sometimes held or flicked their wings over their abdomen. Females prevented mounted males from copulating by either kicking with their hind legs or pushing the tip of their oviscape to the substrate, or both. Females did this while stationary or while dragging the male.

Discussion

Courtship and agonistic displays.—*A. mexicana* appears to share a number of wing displays with other *Aciurina* species as well as other fruit flies in general. Tauber and Tauber (1967) described wing movements of *A. ferruginea* that are similar to the slow signal of *A. mexicana*. They suggested that the display functioned in intraspecific recognition, courtship, and copulation. This

display also was reported for *A. ferruginea* by Wangberg (1981). Dodson (1987b) described similar wing movements for *A. trixa*. The slow signal of *A. mexicana* occurred when flies were together or alone and could not be associated with any specific activity. Slow signals were often seen while flies, regardless of sex, faced each other at a short distance. This suggests that slow signals may in part operate in conspecific recognition. A similar display occurs in a number of fruit flies (e.g. Nation 1972, Piper 1976, Cavender and Goeden 1982, 1984).

Displays like wing fanning and wing flicking may also occur in *A. bigeloviae* (Cockerell) and *A. trixa* (G. Dodson pers. comm.). "Rowing" of the wings described for *A. trixa* (Dodson 1987b) is similar to wing fanning and wing flicking described here (G. Dodson pers. comm.).

Wing fanning by *A. mexicana* may help direct male odor toward intruders. Dispersal of a sex pheromone by a similar behavior has been suggested for *Anastrepha suspensa* (Loew) and *Ceratitis capitata* (Wiedemann) (Nation 1972, Prokopy and Hendrichs 1979). Alternatively, Sivinski et al. (1984) convincingly demonstrated that wing fanning by males of *A. suspensa* produces sounds that are sexually important, intraspecific signals. No sound was noted during wing fanning by *Aciurina mexicana*.

Wing flicking also may help to disperse and direct male odor. Prior to and intermittently during courtship, males rubbed their hind legs against their abdominal pleura and in turn rubbed their wings. This may transfer odor from the pleura to the wings where it then could be dispersed by wing flicking. The activity may be coincidental with grooming. Male *Anastrepha suspensa* exhibit a similar behavior, and Nation (1972) noted that "this cleaning behavior may spread a sex attractant over the body and wings and provide a greater surface from which it can evaporate." Piper (1976) suggested that wing movements in general may help direct pheromones toward either sex.

Copulating males of *Aciurina ferruginea* may "flick" their wings at approaching males (Tauber and Tauber 1967). In the context of agonistic behavior, this display is similar to the wing thrusts of *A. mexicana*. Sparring, but not wing thrusts, has been reported for *A. trixa* (as "grappling," Dodson [1987b]). A display resembling wing thrusts also has been reported for *Trupanea bisetosa* (Coquillett) and *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1982, 1984). In these flies, however, the display functions in courtship.

Wing displays comparable to wing waving have been reported for *A. ferruginea* and *A. trixa* (Tauber and Tauber 1967, Dodson 1987b) as well as other fruit flies (e.g. Tauber and Toschi 1965, Cavender and Goeden 1982, Dodson 1987b). Dodson (1987b) observed 11 virgin female *A. trixa* to mate after frequently waving their wings ("advertising behavior"). Conversely, none of nine once-mated females exhibited the display (Dodson 1987b). Tauber and Toschi (1965) reported that during the courtship of *Euleia fratria* (Loew), the frequency of "wing waving" and displacement of the wings are indicative of the level of sexual excitation of females. As noted above, frequency and duration of wing waving by *A. mexicana* females was affected by the proximity of a courting male, and males produced nuptial gifts only in the presence of a displaying female.

Although fruit fly wing movements usually are discussed in terms of intraspecific displays, there also is strong evidence for an interspecific role. It was recently shown that wing movement and wing pattern of *Rhagoletis zephyria* Snow and *Zonosemata vittigera* (Coquillett) are important in deterring predation by mimicking the flies' salticid spider predators (Mather and Roitberg 1987, Greene et al. 1987). Further, these authors suggested that spider mimicry may be widespread in the Tephritidae.

Abdominal inflation and odor production have not been reported for other *Aci-*

urina species. Tauber and Tauber (1967) refer to "pumping of the abdomen" in male homosexual encounters of *A. ferruginea*, but it is unclear whether this represents abdominal inflation as discussed here. Abdominal inflation accompanied by odor production has been observed in males of the fruit flies *Dirioxa* (= *Rioxa*) *pornia* (Walker), *Anastrepha ludens* (Loew), *A. suspensa*, *Trupanea bisetosa*, and *Toxotrypana curvicauda* Gerstäcker (Pritchard 1967, Nation 1972, Cavender and Goeden 1982, Landolt et al. 1985, Robacker and Hart 1985b). Appearance of the inflated pleura of *Aciurina mexicana* was quite similar to that illustrated for *T. bisetosa* (Cavender and Goeden 1982, Fig. 2).

Glandular epidermal cells have been identified in the pleura of abdominal segments 3, 4, and 5 of males of *D. pornia* (Pritchard 1967), seven *Anastrepha* species, and two *Ceratitis* species (Nation 1981). The cells are sex-specific, occurring as a thick band in male pleura; female pleural epidermis is uniformly thin and undifferentiated (Pritchard 1967, Nation 1981). These glandular cells are, at least in part, the probable source of male odor in *D. pornia*, *A. suspensa*, and *A. ludens* (see Pritchard 1967, Nation 1974, 1981; Robacker and Hart 1985a). Pleura removed from male *Aciurina mexicana* were visibly thicker than those removed from females when compared under a dissecting microscope, regardless of the size of the fly. Based on the above observations, and because odor was detectable only when the pleura were distended, it is likely that the pleura of male *A. mexicana* contain glandular cells that are associated with the male odor.

Odors produced by male *D. pornia*, *Anastrepha suspensa*, *A. ludens*, and *Toxotrypana curvicauda* are attractive to females (Pritchard 1967, Nation 1983, Landolt et al. 1985, Robacker and Hart 1985a). The odor produced by *Trupanea bisetosa* is presumably also a sex pheromone (Cavender and Goeden 1982). Courting males of *Aciurina mexicana* always produced odor, but it was not shown that the odor was attractive to females. Because male odor was produced during wing fanning, it may also function intrasexually.

The male odor of *A. mexicana* is distinctive, but difficult to describe precisely. The male odor of *T. bisetosa* was reported as a "yeasty or musty smell" (Cavender and Goeden 1982). The odor of *A. mexicana* is likewise yeasty or musty.

Nuptial feeding has not been reported for other *Aciurina* species. Dodson (1987b) reported that adult feeding in general is "negligible" for *A. trixa*. He also noted that no flowers or "obvious exudates" occur on the host plant (*Chrysothamnus nauseosus* [Pallas] Britton) when adults are present. In contrast, flies used in the present study often became so replete with the honey/yeast mixture that ordinary movement, let alone mating, was quite limited. Moreover, stems and leaves of *B. sarothroides* are coated with a sticky material that is attractive to many adult insects (Meyer et al. 1979) and on which adult *A. mexicana* may feed. Adults of *A. ferruginea* also feed (Tauber and Tauber 1967).

Nuptial feeding has been observed (Freidberg 1981 and references therein) or suspected (Cavender and Goeden 1984) for a number of fruit flies. In five species, nuptial gifts consist of an erect, white, frothy mass produced from the mouthparts of males and deposited onto the host plant (Freidberg 1981 and references therein). In two of these species nuptial gifts originate in large, sexually dimorphic salivary glands (Pritchard 1967, Freidberg 1981). In *Spathulina sicula* Rondani, a species with postcopulatory trophallaxis, the salivary glands of males are much larger than those of females (Freidberg 1982 [species as *tristis* (Loew)], Fig. 5). Sexually dimorphic salivary glands also are present in males of *Anastrepha* and *Ceratitis* (Nation 1981), but, at least for *A. suspensa*, *A. ludens*, and *C. capitata*, nuptial feeding has not been reported (Nation 1972, Pro-

kopy and Hendrichs 1979, Robacker and Hart 1985b). Preliminary examination of the alimentary tract of five male and five female *A. mexicana* showed essentially no intersexual difference in size and shape of the salivary glands. Both sexes possess a relatively large crop.

Unlike the nuptial gifts discussed above, that of *A. mexicana* consisted of drops of a clear fluid. When initially produced it was similar to the fluid in the crops of dissected flies. The amount of fluid produced was greater than would be expected from the salivary glands alone. It seems probable then, that contents of the crop contributed to the nuptial gift of *A. mexicana*.

Mating behavior.—The courtship posture assumed by male *A. mexicana* has not been reported for other *Aciurina* species. The posture is similar to that illustrated for *D. pornia* (Pritchard 1967, fig. 2). An erect posture also has been observed for *Anastrepha ludens* (Robacker and Hart 1985b).

Mounting and copulatory positions of *A. mexicana* were like those described for *A. ferruginea* (Tauber and Tauber 1967). However, once mounted, males did not contact the female's dorsum with their mouth parts as in *A. ferruginea*. Mounting in *A. trixa* is facilitated by the male grasping the female's hindlegs between the tibia and femur of his forelegs (termed "leglock," Dodson [1987a, b]). The forefemora of males are enlarged and males with larger forefemora are more successful in securing copulations (Dodson 1987a). This method of mounting was not seen for *A. mexicana* and subsequent measurements indicated no significant sexual dimorphism in forefemora (Table 1).

Table 1. Comparison of mean maximum length and width of forefemora among male and female *Aciurina mexicana* (two-tailed *t*-test). Measurements taken with ocular micrometer and dissecting microscope. Means expressed in arbitrary units (35 units = 1 mm).

	$\bar{x}$ (n)	*t*	df	*P*
Femur length				
Males	26.9 (11)	0.37	20	>0.25
Females	26.6 (11)			
Femur width				
Males	8.4 (11)	0.93	20	>0.15
Females	8.1 (11)			

Dodson (1987b) reported multiple matings by female *A. trixa*. Females of *A. mexicana* may also be polyandrous. On one occasion a female mated again after 1 d, while on another occasion a female mated again after 1 wk. Conversely, in two trials initiated 2 d after copulation, one female was unresponsive to and the other actively rejected male courtship. Mean duration of copulation for *A. trixa* (2.2 h [Dodson 1987b]) was longer than that observed for *A. mexicana* (1.5 h).

Evasive actions taken by female *A. mexicana* to prevent copulation are like those described for *A. ferruginea* (Tauber and Tauber 1967) and *A. trixa* (Dodson 1987b). Females of *Anastrepha suspensa* similarly press their oviscape to the substrate to prevent copulation (Nation 1972).

It is unknown to what extent the mating behaviors observed in the laboratory for *Aciurina mexicana* occur in nature. Observation of behavior in the field was unsuccessful because of low fly densities. However, it is very unlikely that the complex behaviors reported here were laboratory artifacts.

Mating behavior and systematics.—*Aciurina mexicana*, *A. aplopappi* (Coquillett), and *A. thoracica* Curran form Steyskal's (1984) *Aplopappi* species group. Unlike other *Aciurina* species, members of the *Aplopappi* group have host plants other than species of *Chrysothamnus*, and lack surface specializations on the membranous portion of sternum 8 of the ovipositor (Steyskal 1984). The observations reported herein raise the possibility that members of the *Aplopappi* group also have distinctive mating behaviors that further distinguish them from the remainder of the genus.

Eldredge and Cracraft (1980) noted that

"with the exception of the findings of comparative anatomy, no other kind of similarity has been utilized by systematists as much as that of behavior." Current supergeneric classifications of the Tephritidae (e.g. Foote and Steyskal 1987), which are based largely on adult morphology, are problematical. It is now well documented that many fruit flies have characteristic mating behaviors. As shown here, sexual displays are a potentially rich (but unused) source of comparative data. The interspecific distribution of these displays may help resolve or corroborate evolutionary patterns used to construct classifications.

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NOMENCLATURE OF SOME NEOTROPICAL GELECHIIDAE (LEPIDOPTERA)

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Abstract.—Five generic and six specific synonymies are established, and 12 new combinations are made. Neotypes are designated for four names and a lectotype for one name. *Symmetrischema tangolias* (Gyen) is established as the valid name for *S. plaesiosema* (Turner), a pest of potato tubers.

Key Words: nomenclature, synonymy, gelechiinae, gelechiid moths, Neotropical Region

Many species and genera of neotropical Gelechiidae have remained unknown since their publication. Meyrick (1925) treated all taxa proposed to that date and made many nomenclatural decisions. In many instances he did so on the basis of written descriptions; he did not see or make an effort to obtain type specimens beyond those in his collection. Clarke (1969a, b) illustrated the adults and genitalia of type specimens of species of Gelechiidae described by Meyrick and held by the British Museum (Natural History). His work is immensely helpful to gain preliminary, and sometimes final, understanding of a large number of species. Becker (1984) relied mainly on literature, original descriptions and revisions, to associate species with genera and to place genera in higher taxa. Because characters necessary to define species and genera in the Gelechioidea often are in the male and/or female genitalia and the number of taxa in the Neotropical Region is very large, many described taxa are unrecognized, sometimes at the family level. This paper, based on study of several type specimens, clarifies knowledge of nine generic names and 18 specific names.

Kieffer and Jörgensen (1910) published on plant galls, the primary gall makers, and parasites reared from the gall makers that had been observed and collected in Argentina (primarily in the province of Mendoza). Nearly all the insects were described as "new species" or as "new genus, new species" combinations. Eight of the insects were Lepidoptera, and four were Gelechiidae. The gelechiid adults were sent to Embrik Strand for description (Strand 1911). He provided manuscript names for the moths to Kieffer and Jörgensen, and they attributed the names to Strand in the text of their paper (Kieffer and Jörgensen 1910). However, they presented adequate information about each species to validate the names and thus became the authors of the Strand names. Because they were not intentionally describing new species and/or genera, they may not have had adults in their possession nor labelled specimens as types. Their descriptions are limited to galls and to larvae or pupae when present; no mention is made of

adult characters. It appears that no type material of these four species is extant in Argentina or elsewhere. The homonymous names published by Strand are supported by specimens provided by Kieffer and are highly suitable to serve as material from which neotypes can be designated. Type material of the Strand names is well preserved in the Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany. We borrowed the types of the Strand names, dissected the abdomens, and endeavored to relate their identities to other taxa. The results follow.

1. *Gnorimoschema* (*Tuta*) *atriplicella* Kieffer & Jörgensen 1910: 363. (Figs. 1, 6).

   The neotype male, present designation, bears the following labels: 1) Argentina/ Mendoza/Kieffer G. 2) male genitalia/ slide 5109/R W Hodges. 3) Neotype by Hodges & Becker 1989.

Gnorimoschema (*Tuta*) *atriplicella* is a valid species of *Phthorimaea* Meyrick, NEW COMBINATION; and it is the type species of *Tuta* Kieffer & Jörgensen. Thus, *Tuta* is a junior synonym of *Phthorimaea*, NEW SYNONYMY; and it is removed from the synonymy of *Gnorimoschema* Busck where Meyrick (1925: 89) had placed it. The moth (Fig. 1) is indistinct, as are most *Phthorimaea*, and has pale yellow-brown forewings and pale straw-yellow hindwings. The male genitalia are as illustrated (Fig. 6).

2. *Tecia mendozella* Kieffer & Jörgensen 1910: 375. (Figs. 2, 7).

   The neotype male, present designation, bears the following labels: 1) Argentina/ Mendoza/Kieffer G. 2) male genitalia/ slide 5107/R W Hodges. 3) Neotype by Hodges & Becker 1989.

Tecia mendozella is a junior synonym of *Topeutis venosa* Butler, NEW SYNONYMY; and it is the type species of *Tecia* Kieffer & Jörgensen. *Topeutis venosa* Butler is the type species of *Orsotricha* Meyrick, which thus becomes a junior synonym of *Tecia*, NEW SYNONYMY; and *Tecia venosa* (Butler) is a NEW COMBINATION.

3. *Fapua albinervella* Kieffer & Jörgensen 1910: 378. (Figs. 3, 8).

   The neotype male, present designation, bears the following labels: 1) Argentinien/ Prov. Mendoza/Kieffer G. 2) male genitalia/slide 5108/R W Hodges. 3) Neotype by Hodges & Becker 1989.

Fapua albinervella is a valid species of *Tecia*, and it is the type species of *Fapua* Kieffer & Jörgensen. Thus, we confirm Meyrick's (1925: 89) placement of the species and treatment of *Fapua* as a junior synonym of *Tecia*. The wing pattern of the moth (Fig. 3) superficially resembles that of a species of *Coleophora* Hübner (Coleophoridae). The forewings are pale yellow orange with white on the veins; the hindwings are pale yellow with a pale-orange fringe.

4. *Tecia* (*Lata*) *kiefferi* Kieffer & Jörgensen 1910: 398. (Figs. 4, 9).

   The neotype male, present designation, bears the following labels: 1) Argentinien/ Prov. Mendoza/Kieffer G. 2) male genitalia/slide 5110/R W Hodges. 3) Neotype by Hodges & Becker 1989.

Tecia (*Lata*) *kiefferi* is a valid species of *Tecia*, and it is the type species of *Lata* Kieffer & Jörgensen. Thus, we confirm Meyrick's (1925: 89) placement of the species and treatment of *Lata* as a junior synonym of *Tecia*. The moth (Fig. 4) is similar to *Tecia venosa* (Butler); however, in the male genitalia (Fig. 9) the anteromesial margin of the tegumen is straight in *kiefferi*; it is rounded in *venosa* (Fig. 2).

Another hitherto unrecognized, monotypic genus is *Brachypsaltis* Meyrick with type species *subalbata* Meyrick. The holotype male of *subalbata* (Fig. 5) was borrowed from the Naturhistorisches Museum, Vienna, and the genitalia were dissected. *B. subalbata* proves to be a valid species of

Figs. 1–5. Wings of Gelechiidae species. 1, *Phthorimaea atriplicella* (Kieffer & Jörgensen), neotype, m, Argentina. 2, *Tecia venosa* (Butler), [neotype of *Tecia mendozella* (Kieffer & Jörgensen)], m, Argentina. 3, *Tecia albinervella* (Kieffer & Jörgensen), neotype, m, Argentina. 4, *Tecia kieffери* (Kieffer & Jörgensen), neotype, m, Argentina. 5, *Tecia subalbata* (Meyrick), holotype, m, Argentina.

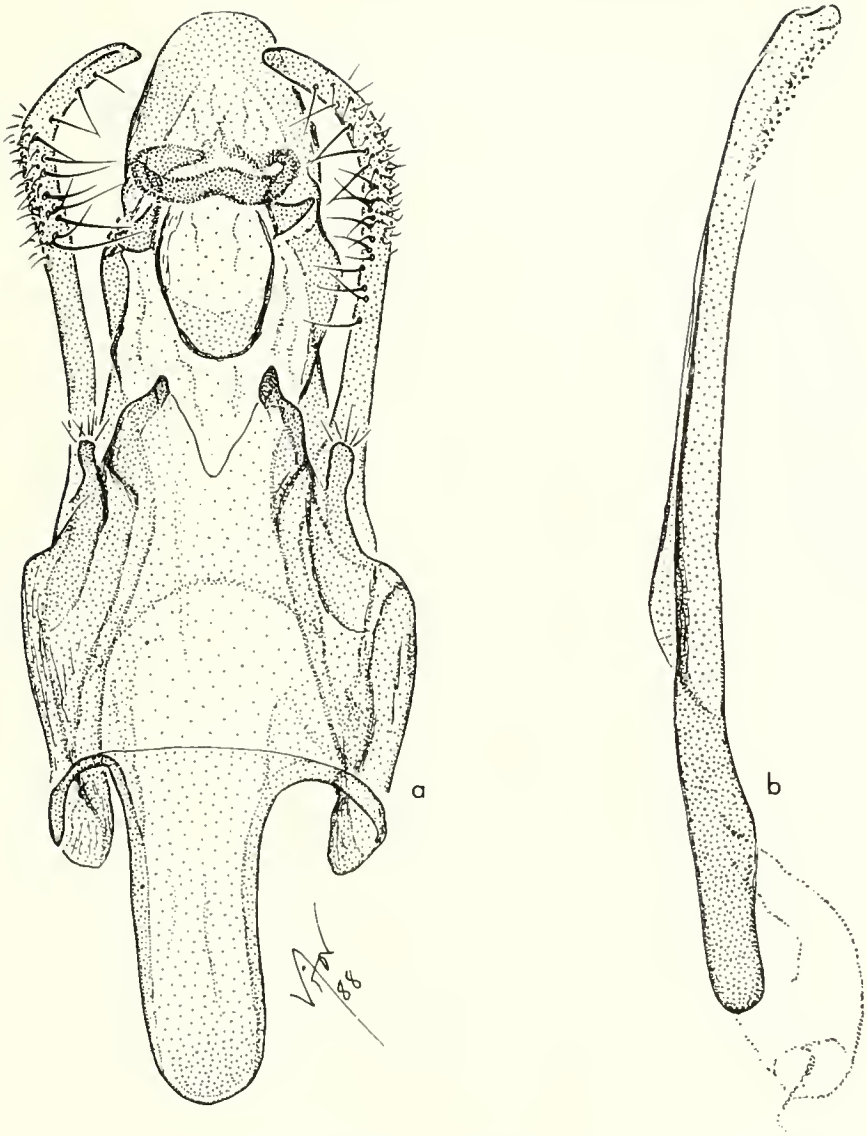

Fig. 6. *Phthorimaea atriplicella* (Kieffer & Jörgensen), neotype, m, Argentina. a, genitalia with aedeagus removed (ventral aspect). b, aedeagus.

Tecia and is transferred to that genus as *Tecia subalbata* (Meyrick), NEW COMBINATION. Thus, *Brachypsaltis* becomes a junior synonym of *Tecia*, NEW SYNONYMY. The male genitalia are as illustrated (Fig. 10).

Becker borrowed eight syntypes of *Holcocera baccharisella* Brèthes from the Museo Argentino de Ciencias Naturalis "Bernardino Rivadavia," Buenos Aires. Brèthes did not indicate the provenance nor the number of specimens he had when he described *baccharisella*. The syntypes bear the same labels: 1) Bs Aires/iv.1916/J.B. 2) *Holcocera baccharisella* Br. We designate a male as lectotype and have added a third

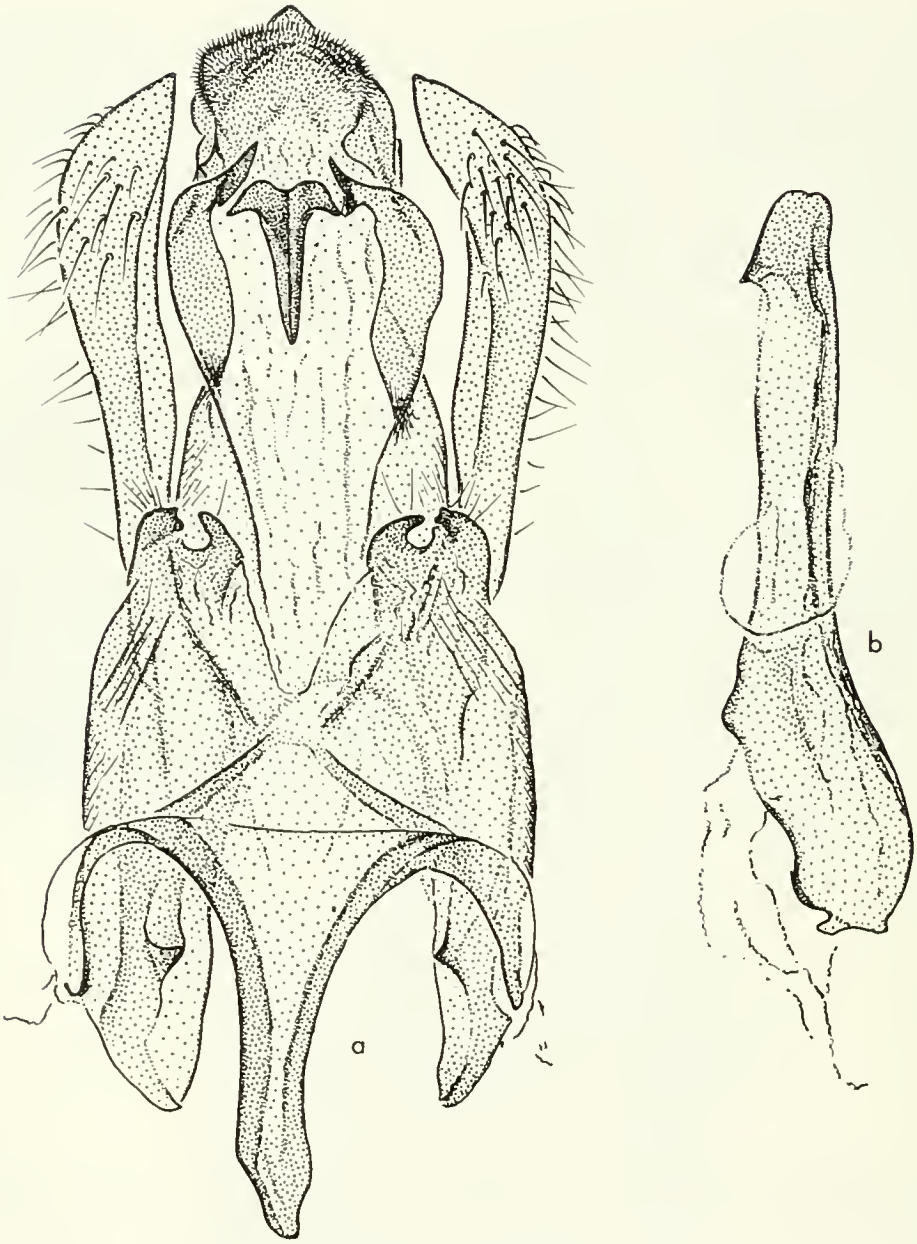

Fig. 7. *Tecia venosa* (Buller), [neotype of *Tecia mendozella* (Kieffer & Jörgensen)], m, Argentina. a, genitalia with aedeagus removed (ventral aspect). b, aedeagus.

label, Lectotype by Hodges & Becker 1989, to it. Paralectotype labels were added to the remaining seven specimens. Study of the male genitalia of *baccharisella* shows it to be a junior synonym of *Topeutis venosa* Butler, NEW SYNONYMY. It is thus transferred to *Tecia* as *Tecia baccharisella* (Brèthes), NEW COMBINATION.

Povolný (1980) described *Scrobipalpopsis* (*Scrobischema*) *vergarai* on the basis of

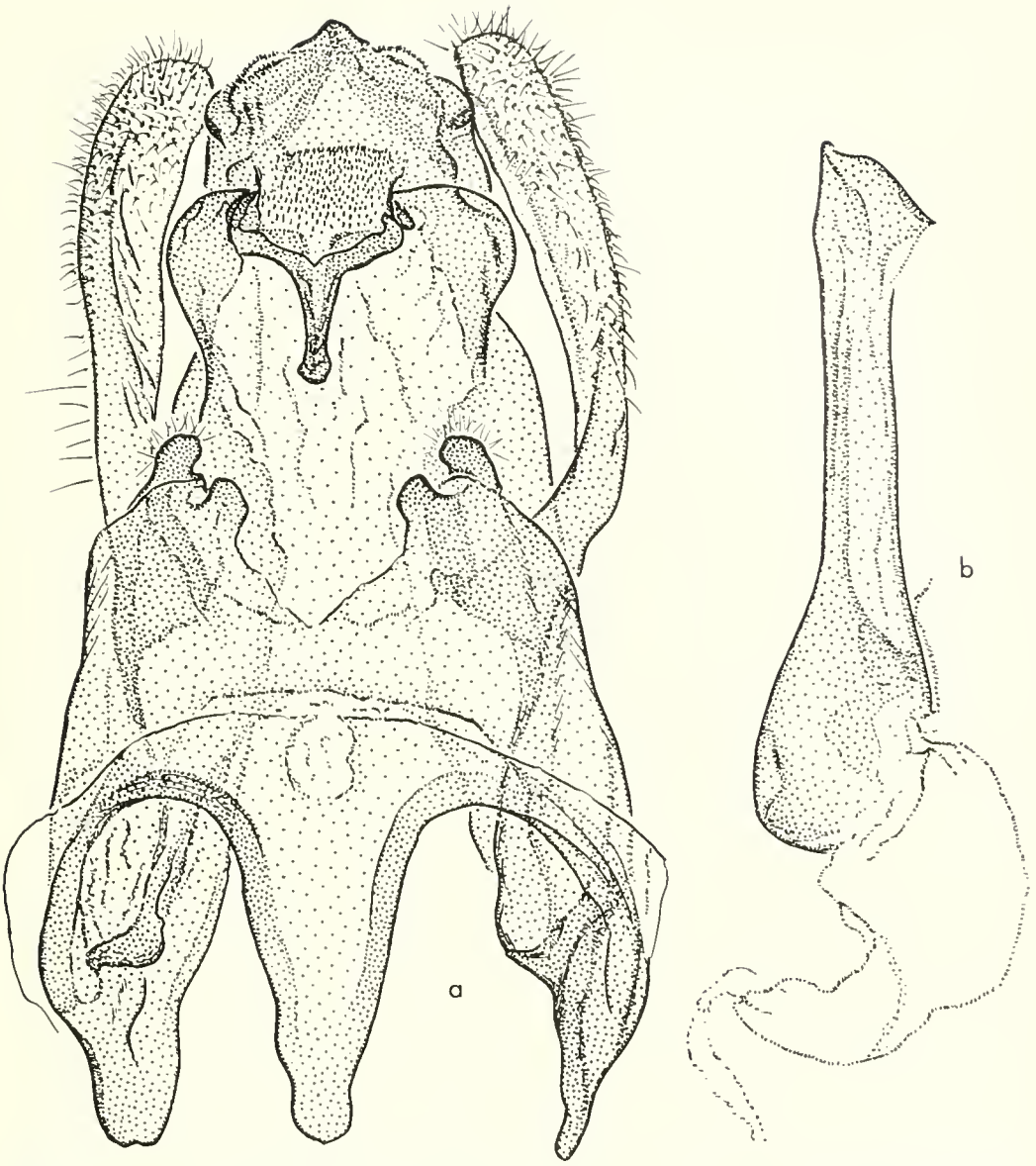

Fig. 8. *Tecia albinervella* (Kieffer & Jörgensen), neotype, m, Argentina. a, genitalia with aedeagus removed (ventral aspect). b, aedeagus.

adults reared from larvae that caused "... hyperplastic deformation of the terminal shoots of *Baccharis macrantha* HBK." *Tecia venosa* is a gall maker on *Baccharis serrulata* Pers. (Kieffer & Jörgensen 1910: 375). Study of Povolný's illustrations and discussion convince us that *S. vergarai* is a junior synonym of *T. venosa*, NEW SYNONYMY. Further, because *vergarai* is type species of *Scrobischema* Povolný, the latter is a junior synonym of *Tecia*, NEW SYNONYMY; and *Tecia vergarai* Povolný is a NEW COMBINATION.

Study of the male and female genitalia of

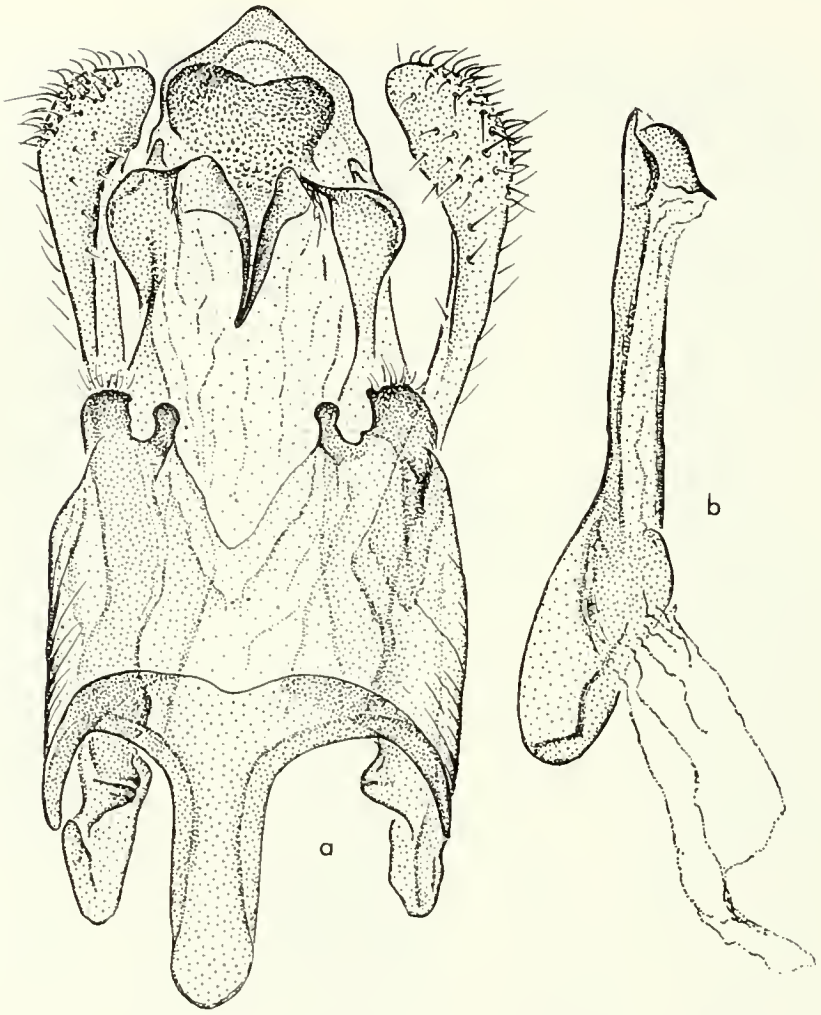

Fig. 9. *Tecia kiefferi* (Kieffer & Jörgensen), neotype, m, Argentina. a, genitalia with aedeagus removed (ventral aspect). b, aedeagus.

Gelechia petasitis Pfaffenzeller, the type species of *Scrobipalpopsis* Povolný, lead us to the conclusion that *Scrobipalpopsis* is a junior synonym of *Tecia*, NEW SYNONYMY, and that *Gnorimoschema tetradymiella* Busck, *Gnorimoschema petrella* Busck, *Gnorimoschema arnicella* Clarke, "*Scrobipalpopsis*" *chili* Povolný, and *Scrobipalpopsis solanivora* Povolný are NEW COMBINATIONS in *Tecia*.

Hodges (1983: 22) erred in making *Scrobipalpopsis* a junior synonym of *Ptycerata* Ely. He used a very similar, but incorrectly identified, specimen for his concept of *Ptycerata busckella* Ely, the type species of *Ptycerata*. The genitalia of the holotype of *Ptycerata busckella* Ely show that it is related to *Monochroa* Heinemann and *Isophrictis* Meyrick, not to *Gnorimoschema* Busck and allies.

Scrobipalpa Janse, with type species *Gelechia heliopa* Lower, is also very similar to

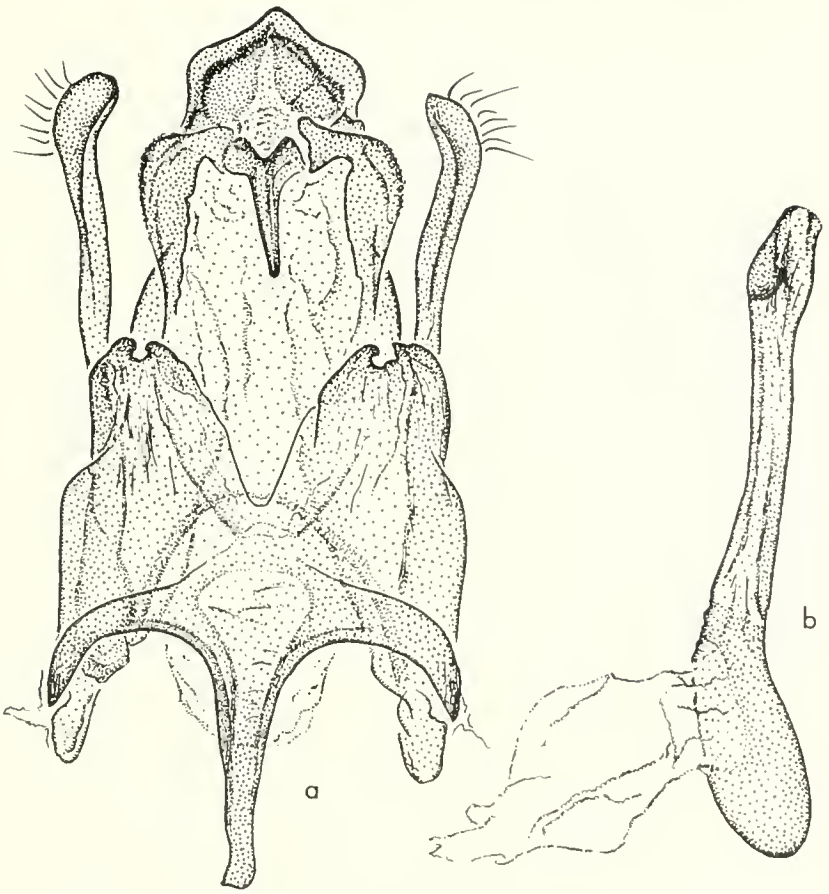

Fig. 10. *Tecia subalbata* (Meyrick), holotype, m, Argentina. a, genitalia with aedeagus removed (ventral aspect). b, aedeagus.

Tecia. We do not propose to synonymize *Scrobipalpa* with *Tecia* at this time; however, we draw attention to the similarity.

Trichotaphe tangolias Gyen has remained in *Trichotaphe* Clemens (Becker 1984: 51), which is a junior synonym of *Dichomeris* Hübner (Hodges 1986: 10), because no type material has been recognized subsequent to the original description. In the U.S. National Museum of Natural History we found a microscope slide with the left wings of *Gelechia* (*Trichotaphe*) *tangolias* Gyen made by Busck in 1916 from a specimen received from Prof. Silva Figueroa of Chile. The forewing definitely is that of *Symmetrischema plaesiosema* (Turner). Gyen's paper (1913) indicates that he received the specimens on which the description was based from C. Silva Figueroa. A few pages further on, in the same publication, Silva (1913) published on the life history of *T. tangolias*, illustrating the immature stages on potato. Silva (1915) published a short note and illustrated the adult, pupa, and larva of *Trichotaphe tangolias*. The illustration of the adult is a crude representation of *S. plaesiosema*. On the basis of the original description, the pair of wings received from Silva, the host, and the illustration by Silva, we conclude that *Trichotaphe tangolias*

Gyen is a senior synonym of *Symmetrischema plaesiosema* (Turner), NEW SYNONYMY, and is a species of *Symmetrischema* Povolný [*Symmetrischema tangolias* (Gyen), NEW COMBINATION].

Nomenclatural Summary

GELECHIIDAE
Gelechiinae
Phthorimaea Meyrick 1902
Tuta Kieffer & Jörgensen 1910, n. syn.
[from Gnorimoschema]
atriplicella (Kieffer & Jörgensen 1910), n. comb.
[from Gnorimoschema]

Symmetrischema Povolný 1967
tangolias (Gyen 1913), n. comb.
[from Trichotaphe]
plaesiosema (Turner 1919), n. syn.
melanoplintha (Meyrick 1926), n. syn.
tuberosella (Busck 1931), n. syn.

Tecia Kieffer & Jörgensen 1910
Fapua Kieffer & Jörgensen 1910
Lata Kieffer & Jörgensen 1910
Orsotricha Meyrick 1914, n. syn.
Brachypsaltis Meyrick 1931, n. syn.
Scrobipalpopsis Povolný 1967, n. syn.
[from Ptycerata]
Scrobischema Povolný 1980, n. syn.
albinervella (Kieffer & Jörgensen 1910)
arnicella (Clarke 1942), n. comb.
[from *Ptycerata*]
chili (Povolný 1967), n. comb.
[from Ptycerata]
kiefferi (Kieffer & Jörgensen 1910)
petasitis (Pfaffenzeller 1867), n. comb.
[from Scrobipalpopsis]
petrella (Busck 1915), n. comb.
[from Ptycerata]
solanivora (Povolný 1973), n. comb.
[from Ptycerata]
subalbata (Meyrick 1931), n. comb.
[from Brachypsaltis]
tetradymiella (Busck 1903), n. comb.
[from Ptycerata]
venosa (Butler 1883), n. comb.
[from Orsotricha]
mendozella (Kieffer & Jörgensen 1910), n. syn.
baccharisella (Brèthes 1917), n. syn., n. comb.
[from Holcocera, Blastobasidae]
vergarai (Povolný 1980), n. syn., n. comb.
[from Scrobischema]

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THREE NEW SPECIES OF MICROCADDISFLIES (TRICHOPTERA: HYDROPTILIDAE) FROM THE OZARK MOUNTAINS, U.S.A.

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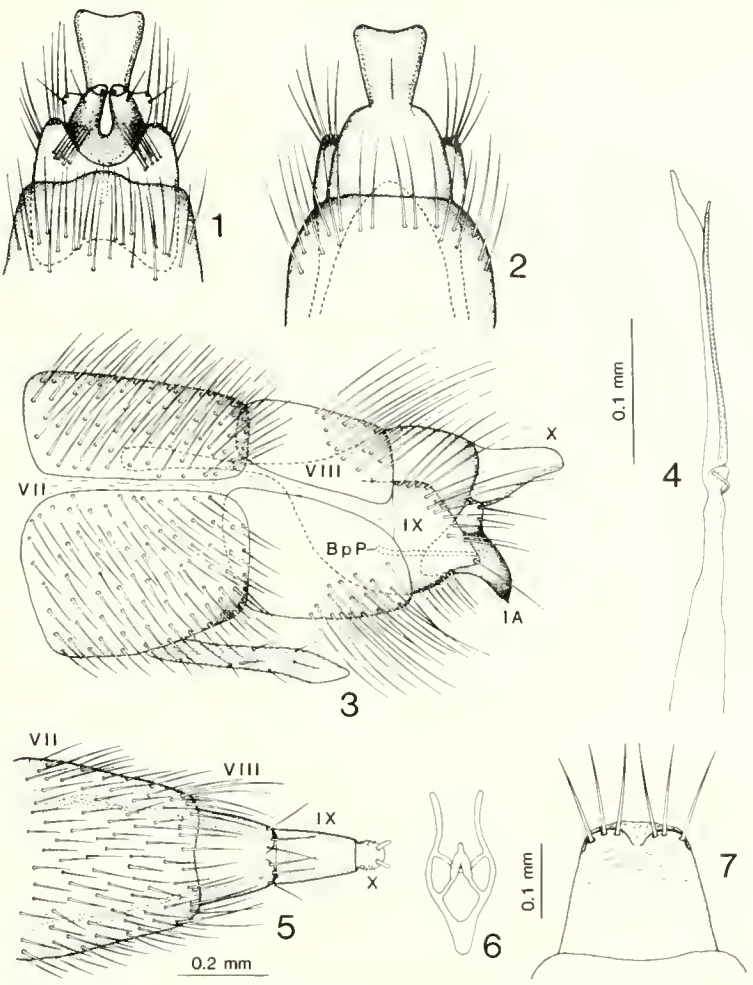
Abstract.—Three new species of hydroptilid caddisflies are described from the Ozark Mountains of Arkansas and Missouri. ***Hydroptila artesa*** n. sp. and ***H. sandersoni*** n. sp. are members of the *H. tineoides* species group and are closely related to *H. amoena, H. paramoena,* and *H. oneili.* A key separating these five species is presented. *Neotrichia arkansasensis* n. sp. is most closely related to *N. sonora* from the desert Southwest, but is easily distinguished by the shape of the inferior appendages.

Key Words: microcaddisfly, *Hydroptila tineoides* group, taxonomic key, Ozark Mountains, new species

The Interior Highlands encompasses mountainous areas of southern Missouri, northern Arkansas, eastern Oklahoma, eastern Kansas, and southwestern Illinois. The region includes the Ozark and Ouachita Mountains and a number of smaller ranges in Oklahoma and Kansas. Much of the area in Arkansas, Oklahoma, and Missouri is undeveloped or used for light agricultural purposes such as livestock ranching. Streams and springs are abundant and many are unpolluted. The area includes five streams classified as National Scenic Riverways and some of the largest volume springs in North America. Surprisingly, the region is one of the more-poorly studied areas in the United States with regard to its trichopteran fauna. Only Kansas and northwest Arkansas have been sampled intensively (Unzicker et al. 1970, Schuster and Hamilton 1978, Hamilton and Schuster 1978, 1979, 1980, Hamilton et al. 1983). In order to increase our knowledge of the trichopteran fauna of this region, we have initiated surveys in the mountainous areas of Arkansas, Missouri, and Oklahoma. We describe herein three new microcaddisflies collected from the Ozark Mountains.

Specimens were collected using a UV-light trap with the exception of a single sample from Mammoth Springs, Arkansas, that we obtained from the Illinois Natural History Survey. Terminology and higher taxonomy follow Marshall (1979). In characterizing some species, we use the ratio of the length of the aedeagus to that of the abdomen. The length of the abdomen was measured dorsally from the posterior margin of the metascutellum to the apex of tergite X. Types and voucher specimens are deposited at the American Museum of Natural History (AMNH), Illinois Natural History Survey (INHS), National Museum of Natural History, Smithsonian Institution (NMNH), and University of Arkansas Insect Collection (UAIC).



Figs. 1–7. *Hydroptila artesa*. Figs. 1–4. Male genitalia. 1, Ventral. 2, Dorsal. 3, Lateral. 4, Aedeagus (lateral). Figs. 5–7. Female genitalia. 5, Ventral. 6, Internal apparatus. 7, Eighth sternite (ventral). IA, Inferior Appendage; BpP, Bilobed Process.

Hydroptila artesa Mathis and Bowles
New Species
Figs. 1–7

This species belongs to the *H. tineoides* group and is most similar to *H. paramoena* Harris. The new species is distinguished from the latter species by the shape of tergite X, inferior appendages, and aedeagus.

Male.—Length 1.9–2.8 mm. Antennae 30–34-segmented. Color yellowish brown in alcohol. Abdominal segment VII with long ventral process extending to middle of segment VIII. Segment IX with dorsum broadly rounded, lacking setae; with narrow lateral lobe bearing apical setae; excised deeply anterodorsally and gently postero- and anteroventrally; apodeme long and narrow, arising from dorsal one-half of segment, extending into, but never past segment VII. Segment X fused dorsally with segment IX; lateral margins lightly sclerotized; hood-shaped in lateral view, but not sharply upturned, widening posteriorly in dorsal view, apex emarginate. Inferior ap-

pendages short, beak-like, relatively wide in lateral view; distal portion separated and basal portion fused along meson in ventral view; with broad, thumb-like dorsal projection bearing long setae. Bilobed process present. Aedeagus short, less than one-third length of abdomen; widest at base, with two long, apical processes; process bearing ejaculatory duct long and slender, duct protruding at apex; other process flattened and pointed apically; titillator spirally one-third turn anteriorly.

Female.—Length 2.4–3.4 mm. Antennae 22–26-segmented. Similar to male in general appearance. Abdominal segment VI with broad, spur-like ventral process. Abdomen with three pairs of apodemes; posterior-most pair extending length of segment IX; mesial pair with anterior end expanded and curved toward midline, extending from posterior margin of segment VIII into anterior one-half of segment VII; lateral pair straight, extending from posterior margin of segment IX to posterior margin of segment VI. Segment VIII tapering; sternite with pair of sclerotized lobes posteriorly, each bearing 3 (rarely 4) stout setae, membranous anterior to lobes. Segment IX tapering slightly. Segment X short, ovoid; bearing pair of short cirri subterminally and numerous small setae. Internal apparatus lyre-shaped, with a star-like mesial configuration.

Immatures.—Unknown.

Etymology.—French, referring to the typical spring habitat of the species.

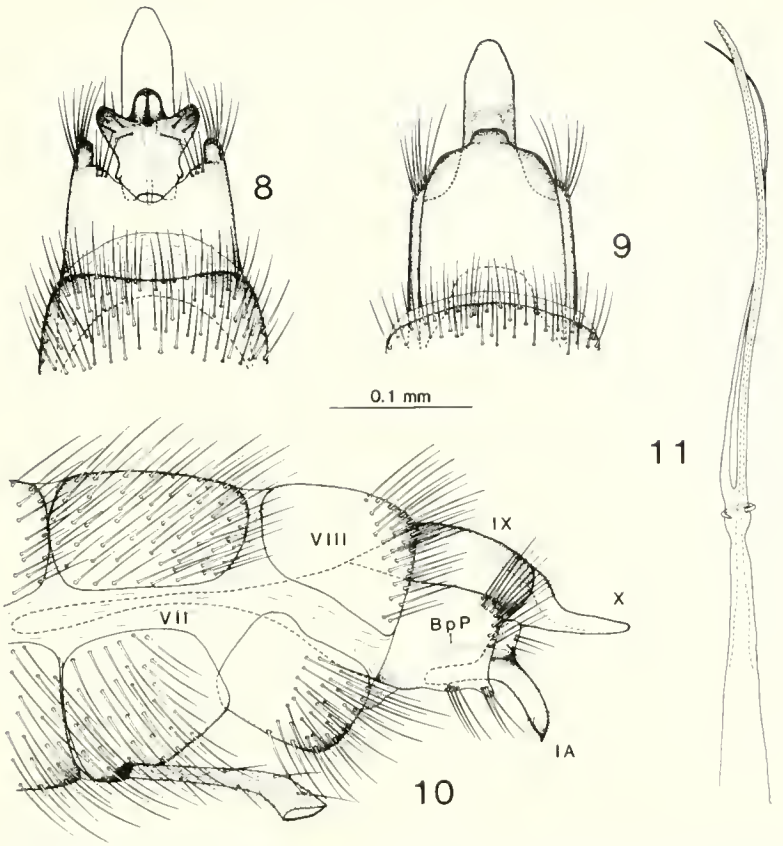
Holotype, male and allotype.—Missouri, Shannon County, Alley Spring, Ozark National Scenic Riverways (O.N.S.R.), 5 mi W Eminence, Hwy 106, 16 August 1987, M. Mathis, S. Tedder (NMNH).

Paratypes.—Same data as holotype, 18 ♂♂, 9 ♀♀ (NMNH, INHS, UAIC); Carter County, Big Spring, O.N.S.R., 7 mi S Van Buren, Hwy 103, 18 August 1987, 15 ♂♂, M. Mathis, S. Tedder (INHS, NMNH); Dent County, Current River, Montauk State Park, 23 mi SE Salem, Hwy 119, 15 October 1988, 7 ♂♂, M. Mathis, D. Bowles (INHS); Oregon County, Eleven Point River, Hwy 19 bridge, 1.5 mi NE Greer, 6 July 1988, 8 ♂♂, M. L. Mathis, D. E. Bowles (NMNH); Ozark County, Althea Spring, 8 mi NW Caulfield, H Hwy, 8 August 1988, 5 ♂♂, M. Mathis, S. Tedder, L. Tedder (AMNH); Ozark County, North Fork White River, H Hwy bridge, 8 mi NW Caulfield, 8 August 1988, 10 ♀♀, 8 August 1988, M. Mathis, S. Tedder, L. Tedder (AMNH, INHS); Arkansas, Fulton County, Mammoth Spring, 19 July 1969, 4 ♂♂ (INHS).

Discussion.—Males of *Hydroptila artesa*, as well as those of *H. amoena* Ross, *H. paramoena*, and *H. oneili* Harris, have a long ventral process on abdominal segment VII, beak-like inferior appendages, and the phallus divided into two apical processes. *Hydroptila hamata* Morton also has been reported to share these characters, but close examination will reveal a third, spur-like apical phallic process (see Ross 1944; fig. 512D). *Hydroptila artesa* differs from all three species in that the phallus is less than one-third the length of the abdomen and the apical phallic process that lacks the ejaculatory duct is flattened into a broad pointed apex. It is distinguished easily from *H. paramoena*, the most closely related species, in that tergite X is not upturned strongly in lateral view, becomes wider posteriorly and is broadly excised in dorsal view, and the inferior appendages are separated along the meson. Females of *H. artesa* may be distinguished from those of *H. amoena* by the presence of a pair of subterminal lobes on sternite VIII rather than well-developed ovate plates. They differ from those of *H. hamata* in lacking a pair of transverse sclerotized bars anterior to the apex of sternite VIII.

Hydroptila sandersoni Mathis and Bowles
NEW SPECIES
Figs. 8–11

This species, like the preceding one, is a member of the *H. tineoides* group and is most closely related to *H. oneili* and *H. amoena*. It is distinguished by the shape of



Figs. 8–11. *Hydroptila sandersoni*, male genitalia. 8, Ventral. 9, Dorsal. 10, Lateral. 11, Aedeagus (lateral). IA, Inferior Appendage; BpP, Bilobed Process.

tergite X, inferior appendages, and the length of the apodemes.

Male.—Length 2.1–2.3 mm. Antennae 29–30-segmented. Color brown in alcohol. Abdominal segment VII with long, medial, ventral process extending to posterior margin of segment VIII. Segment VIII short, flexed ventrally. Segment IX excised deeply anterodorsally and ventrally and shallowly posteroventrally; dorsum broadly rounded, setation absent; with long narrow lateral lobe bearing many setae along posterior and ventral margins; apodeme long, narrow, extending into segment VI. Tergite X long and slender in dorsal view, tapering posteriorly, apex complete; cap-shaped in lateral view, apex straight or slightly up-turned; fused dorsomedially to posterior of tergite IX, ventrally to lateral lobes of segment IX. Inferior appendages "beak-like," with dorsolateral thumb-shaped projection bearing several setae; main axis slender in lateral view, fused basally and contiguous along meson in ventral view. Bilobed process short. Aedeagus widest basally, produced into two slender apical processes; process bearing ejaculatory duct thicker of two, gently curving dorsally; ejaculatory duct not protruding or bent; apex of other process narrow, curving sharply dorsally; titillator turning three-quarter revolution anteriorly.

Female.—Unknown.

Immatures.—Unknown.

Etymology.—Named in honor of Dr. Milton W. Sanderson for his many contributions to the study of Trichoptera.

Holotype.—Arkansas, Stone County, Sylamore Creek, Gunner Pool Recreation Area, 20 July 1988, C. Carlton, R. Leschen (NMNH).

Paratypes.—Same as above, 1 ♂ (NMNH); same, but 22 July 1987, 2 ♂ (UAIC); Johnson County, Mulberry River, 5 mi W Oark, Hwy 215, 23 July 1986, 1 ♂, D. Bowles (INHS); Carrol County, Osage Creek, Hwy 68 bridge, 4 August 1985, 1 ♂, D. Bowles, M. Mathis (INHS).

Discussion.—*Hydroptila sandersoni* bears a close resemblance to both *H. amoena* and *H. oneili*, but differs in a number of features. Unlike these species, tergite X of *H. sandersoni* is slender and complete apically, the ventral axis of the inferior appendages is narrow in lateral view, and the apodemes of segment IX are relatively longer and always extend into segment VI. The apex of the ejaculatory duct of *H. sandersoni* is straight and does not protrude, but in *H. oneili*, it is protruding and bent. *Hydroptila sandersoni* was collected from the headwater reaches of warm-water streams in northern Arkansas.

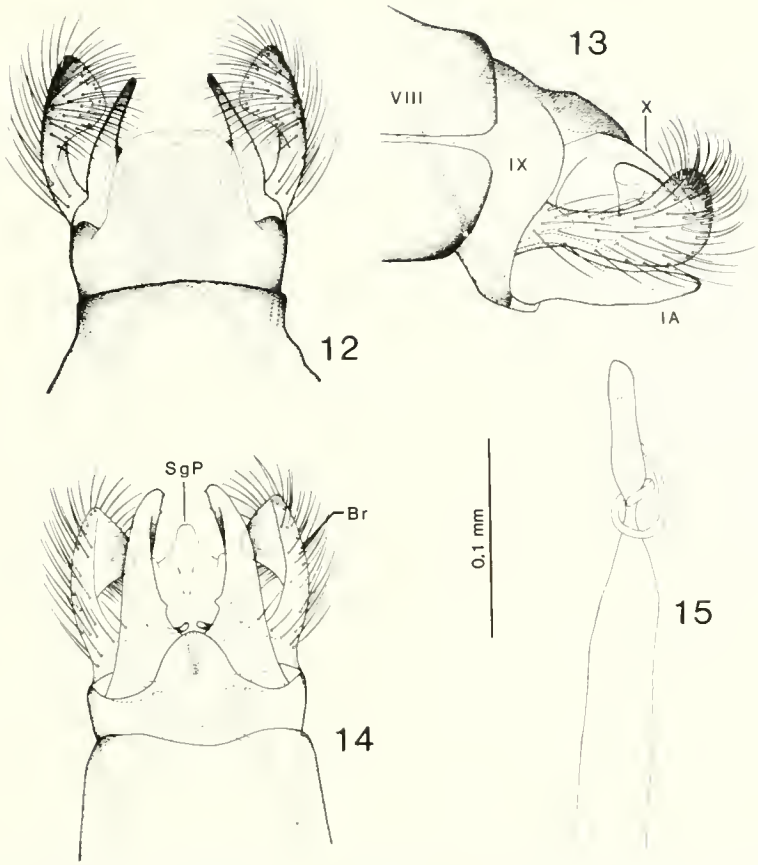
The *H. tineoides* species group encompasses 20 species, all of which are Nearctic except *H. tineoides* Dalman (Palaearctic) and *H. moselyi* Ulmer (Oriental). In this group, the inferior appendages are somewhat C-shaped, typically consisting of a short, beak-like ventral axis and a broad dorsolateral projection bearing one or more long setae. The distal portion of the aedeagus is divided into two or three processes that may be variously modified. Tergite X is well-developed and usually hood-shaped in lateral view. The medial process of sternite VII may be short and spur-like or elongated. A bilobed process is present in at least some species. Within the *tineoides* group there are five species that closely resemble *H. amoena*. In these species, the medial process of sternite VII is elongate, a bilobed process is present, and the aedeagus is divided into two long, slender apical processes. Following is a key to the Nearctic species of the *H. tineoides* group that are identified as *H. amoena* using either Ross (1944) or Blickle (1979).

1. Aedeagus short, less than one-third as long as abdomen; phallic process lacking ejaculatory duct with apex flattened and pointed .. *H. artesa*
– Aedeagus longer, greater than one-third as long as abdomen; apical process not as above 2
2. Apex of tergite X complete; ventral axis of inferior appendage slender ..... *H. sandersoni*
– Apex of tergite X excised; ventral axis of inferior appendage stout 3
3. Apex of tergite X with deep, wide excision (see Harris 1985; fig. 8E); tips of phallic processes simple ..... *H. amoena*
– Apex of tergite X only slightly emarginate; phallic process bearing ejaculatory duct with tip modified or bent 4
4. Tergite X strongly upturned in lateral view (see Harris 1985; fig. 8A); phallic process with an apical, rattle-like structure (see Harris 1985; fig. 8D) ..... *H. paramoena*
– Tergite X only slightly upturned in lateral view (see Harris 1985; fig. 9A); phallic process with ejaculatory duct protruding and noticeably bent (see Harris 1985; fig. 9D) ..... *H. oneili*

Neotrichia arkansasensis
Mathis and Bowles
New Species
Figs. 12–15

Neotrichia arkansasensis closely resembles *N. okopa* Ross, *N. sonora* Ross, and *N. osmena* Ross, but it is distinguishable from these species by the shape of tergite X and the inferior appendages.

Male.—Length 2.0–2.4 mm. Antenna 18-segmented. Color brown in alcohol. Abdominal segment VIII small, subquadrate in dorsal view. Segment IX annular, apodeme short; with complex network of internal sclerotization; dorsum membranous, with many small setae; extending posteriorly and covering tergite X. Tergite X consisting of a pair of sclerotized, pointed processes curving posteroventrally and a pair of heavily-sclerotized basal pieces extending ventrally. In dorsal view, basal piece produced into a short, mesial process joined to a concave lateral shoulder; piece sub-



Figs. 12–15. *Neotrichia arkansasensis*, male genitalia. 12, Dorsal. 13, Lateral. 14, Ventral. 15, Aedeagus (dorsal). IA, Inferior Appendage; SgP, Subgenital Plate; Br, Bracteole.

triangular in lateral view. Inferior appendages dark brown to black; tapering throughout length in ventral view, curving slightly dorsad in lateral view; basally with a down-curving, finger-like projection on mesial face and a tooth-like process just posterior to this projection. Bracteoles spatulate, with concave mesial face, bearing many setae. Subgenital process well developed, with rounded mesial lobe flanked on both sides by long setae; bearing two pairs of short setae on midline of ventral surface. Aedeagus with distinct proximal and distal regions; proximal portion long, wide, and cylindrical basally, with a short, tapering neck; distal portion tapering slightly, with a distinct ejaculatory duct and subterminal genital pore; spiral process large, making one revolution anteriorly before extending posteriorly one-half revolution.

Female.—Unknown.

Immatures.—Unknown.

Etymology.—Latin: of Arkansas.

Holotype.—Arkansas, Madison County, Kings River, 5 mi S Kingston, NW ¼, SW ¼, Sect. 4, T 15 N, R 24 W, 2 June 1985, D. Bowles (NMNH).

Paratypes.—Same as above, 1 ♂ (INHS); Johnson County, confluence of Little Piney and Sulfur Creeks, 12 mi N Hagarville, Hwy 123, 7 June 1986, 3 ♂, C. Robotham (NMNH, UAIC); Johnson County, unnamed spring, 5 mi W Oark, Hwy 215, 12 June 1986 1 ♂, D. Bowles (INHS); Sharp

County, Spring Creek, Spring Creek Wildlife Management Area, 8 June 1988, 1 ♂, R. Leschen (UAIC).

Discussion.—*Neotrichia arkansasensis* is most closely related to *N. sonora,* but also shares a number of characters with *N. okopa* and *N. osmena.* In *N. arkansasensis* and *N. sonora,* tergite X is produced into two long, downturning, sclerotized points that are poorly developed in both *N. okopa* and *N. osmena.* The darkly sclerotized base of tergite X viewed laterally forms a large triangular-shaped plate in *N. arkansasensis* and *N. sonora,* but it is reduced in *N. osmena* and forms a narrow point in *N. okopa.* The most outstanding difference between *N. arkansasensis* and *N. sonora* is the shape of the inferior appendages. In *N. arkansasensis,* they are straight or slightly upturned in lateral view, taper throughout their length and are straight or converging in ventral view, and have a finger-like process arising basally from the mesial face. The inferior appendages of *N. sonora* are sharply upturned in lateral view, taper abruptly near the apex and are diverging in ventral view, and have the finger-like process arising near the midlength of the mesial face. The two species also differ in the shape of the sclerotized basal portion of tergite X; in ventral view, it forms a sharply angular triangle in *N. sonora,* but in *N. arkansasensis* it has a concave lateral face and forms a blunt point distally.

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CUBITUS POSTERIOR IN HYMENOPTERA

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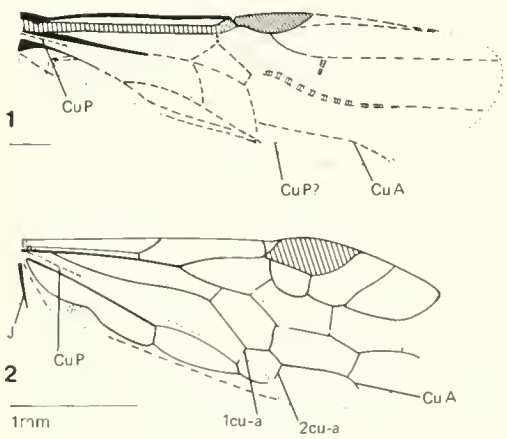
Abstract.—Forewing veins of Hymenoptera named by Ross (1936) Cu, Cu 1, Cu 1a are really Cu A. Ross's vein Cu 1b is a crossvein, 2cu-a, necessitating that Ross's cu-a be called 1cu-a. The rarely seen vein Cu 2 (Ross 1936) in Hymenoptera should be called Cu P. An apparent distal section of Cu P is readily seen in Rhopalosomatidae, and can be seen in spectral form in many other Apocrita.

Key Words: Hymenoptera, venation, wing, Cubitus Posterior, Comstock-Ross system

When Comstock (1895) published his system for naming the veins of Hymenoptera his nomenclature rested on the phylogenetically unsound practice of interpreting the venation of Hymenoptera by comparison with that of higher Diptera (Comstock 1918, p. 383 ff). The serious flaws in the resulting scheme may well have accounted for the general reluctance of hymenopterists of the early 20th century to use Comstock's system (Rohwer and Gahan 1916). These flaws were not corrected until 40 years later when H. H. Ross (Ross 1936) reinterpreted hymenopterous venation by comparing venation of primitive Hymenoptera (Symphyta) with what he then believed to be the most closely related extant orders, Megaloptera, Trichoptera, and Mecoptera. The soundness and brilliance of his interpretation can be seen by the widespread acceptance, with no essential modification, of the Ross system today, over 50 years later.

There were some points about which Ross expressed doubt. One was the identity of the branches of Media and Cubitus. He was familiar with Lameere's and Martynov's system of naming convex veins "anterior" and concave ones "posterior" because he cited Martynov's work and labels veins of many of the non-hymenopterous wings as MA and MP. He decided to call the single Media vein of Hymenoptera "M" mainly for lack of evidence and for convenience. For branches of Cubitus he considered the evidence equivocal, apparently because the posterior branch of the Cubital vein of *Sialis* is neutral in profile, even though falling near the claval furrow in a concave part of the wing. As a compromise he retained the Comstock names for the branches of Cubitus, Cu 1 and Cu 2, the former subdivided into Cu 1a and Cu 1b. Subsequent research has clarified the doubts felt by Ross so that one can no longer justify using Comstock-Ross nomenclature for the branches of Cubitus in Hymenoptera (Carpenter 1966, Wootton 1979, Rasnitsyn 1980). The Lameere hypothesis and its background is best summarized by Carpenter (1966). Comstock's hypothesis is criticized by Lameere and by Martynov (op. cit.). Veins Cu 1 and Cu 2 of the Ross system should be called Cu A and Cu P, respectively, to align hymenopterous vein nomenclature with modern usage and opinion among students of other orders, and especially with usage in



Figs. 1, 2. Symphyta forewings. 1, *Orussus occidentalis* Cr. (Orussidae) to show basal, concave nebular section of Cu P and possible apical, spectral section of Cu P (weakly defined and often absent). 2, *Xyela bakeri* Konow (Xyelidae) to show nebular basal section of Cu P, claval furrow and cu-a crossvein. (Conventions of delineation follow Mason (1986). Scale lines = 1 mm).

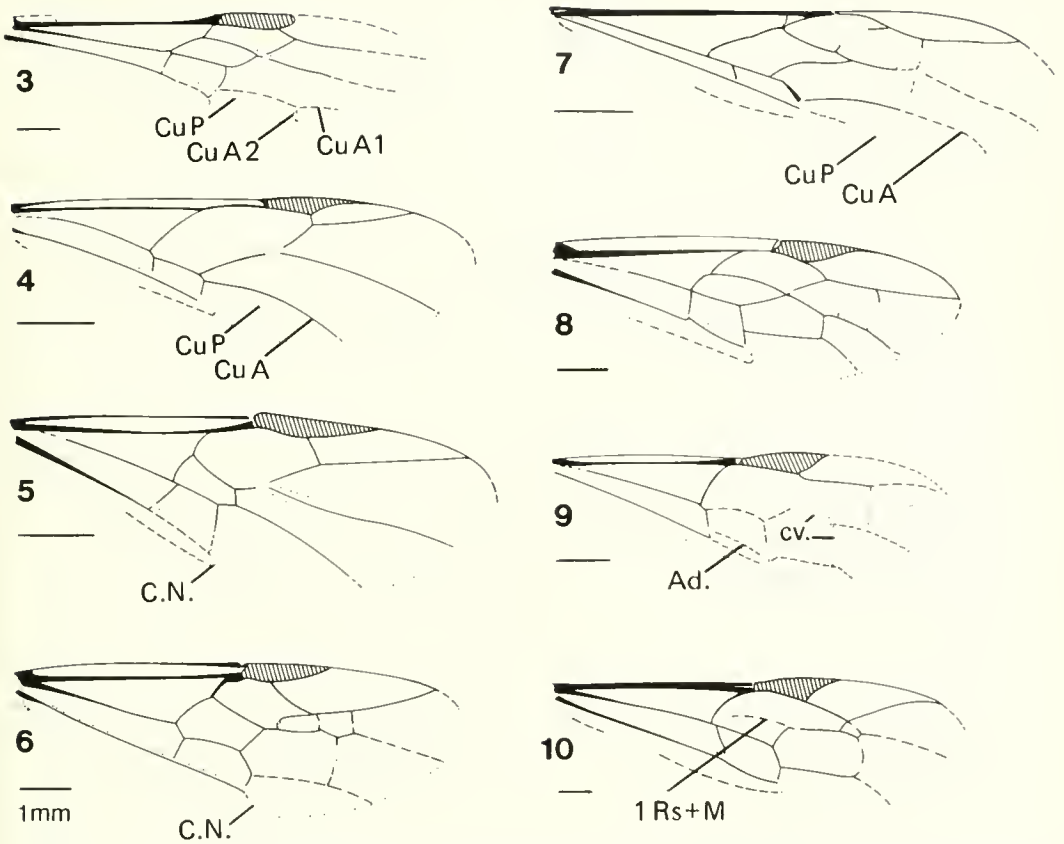
the study of those fossil groups most probably including the sister group of Hymenoptera (Rasnitsyn 1980).

Ross, following Comstock's system, named the two branches of his first cubital vein Cu 1a and Cu 1b. In his figures of non-hymenopterous wings (Ross 1936, figs. 2, 6, 8, 20–22, 24) he shows both Cu 1a and Cu 1b extending to the wing margin far distad of the claval notch (which is found on the margin between the apices of 1A and Cu 2). In his figures of Hymenoptera, however (Ross 1936, figs. 3–5, 23), he shows Cu 1b turning abruptly caudad, crossing the claval furrow, where a bulla is formed, and meeting 1A proximad of the claval notch (Fig. 2). Because the vein called Cu 1b by Ross follows such a radically different course in Hymenoptera compared to that in the older orders, Megaloptera, etc., Ross's interpretation is questionable. Furthermore, if my interpretation of the distal section of Cu P in Hymenoptera is correct (see below), Ross's hypothesis calls for his Cu 1b to cross Cu P and meet 1A, a highly improbable course.

Another interpretation of "Cu 1b" in Hymenoptera is that it is a second cu-a crossvein. The Megaloptera (Ross 1936) and the extinct Miomoptera (Rasnitsyn 1980), groups postulated as possibly ancestral to Hymenoptera, are copiously supplied with crossveins. The second cu-a crossvein in Hymenoptera could well have a compound origin similar to that suggested for the first cu-a by Ross (1936, p. 106), i.e. crossveins extending from Cu A to Cu P and from Cu P to 1A lined up with one another during the reduction and loss of Cu P.

Modern thought (summarized in Wootton 1979) is that Cu P is closely associated with the claval furrow. In light of this it seems to me unreasonable to postulate that Cu A should have a branch crossing the site of Cu P (and the extant claval furrow) to join 1A. I think the existence of a second cu-a crossvein is a more tenable hypothesis for Hymenoptera. A truly branched Cubitus (Cu A1, Cu A2) can be seen in Stephanidae (Fig. 3).

Certainly Cu P existed in the forewing of many extinct Neopterous insects and is easily seen in extant forms, where it closely parallels the claval furrow. Ross (1936) drew attention to the trace (nebulous, Mason 1986) of a concave vein along the basal part of the claval furrow in forewings of Xyelidae and called it Cu 2 (Fig. 2), his equivalent of what recent authorities call Cu P. Significantly, there is a similar nebulous vein in Orussidae (Fig. 1). Recently (Mason 1986), I noticed a usually spectral concave vein in forewings of several groups of Apocrita, running distally from the junction of the claval furrow and 2nd cu-a (= Cu 1b, Ross). Further searching has revealed a concave spectral vein in phylogenetically old members of all apocritous major groups that have most of the venation preserved. At least some species of the following families have the vein present: Stephanidae, Megalyridae, Trigonalidae, Aulacidae, Monomachidae, Roproniidae, Ibaliidae, Cynipidae, Bethylidae, Scolebythidae, Tiphiidae, Sapygidae,



Figs. 3–10. Forewing of diverse Apocrita showing apical trace of Cu P branching from claval furrow. 3, *Schlettererius cinctipes* Cr. (Stephanidae); note 2 branches of Cu A. 4, *Monomachus* sp. (Monomachidae). 5, *Ropronia garmani* Ashm. (Roproniidae). 6, *Orthogonalys pulchella* Cr. (Trigonalidae); note minute jugum. 7, *Liosphex varius* Tow. (*Rhopalosomatidae*); note nebular Cu P, fusion of C and R, retention of lr and loss of stigma. 8, *Pristaulacus* sp. (Aulacidae); note jugum defined by convex wing fold. 9, *Pristocera atra* Klug (Bethylidae); note nebular adventitious vein (Ad.) between 1 cu-a and 2 cu-a, spectral concave combination of vein 2-M and medial furrow, concave spectral 2m-cu, c.v.-concave vein. 10, *Exeristes roborator* Grav. (Ichneumonidae); note nebular 1 − Rs + M, a unique feature for this family. (Conventions of delineation follow Mason (1986). Scale lines = 1 mm).

Anthoboscidae, Vespidae, Bradynobaenidae, Rhopalosomatidae, Astatidae, Hylaeidae, Ichneumonidae (Figs. 3–10). The Cu P vein is so widespread among primitive Apocrita that I suggest it to be a basic character of the Apocrita. The absence of the "vein" in Symphyta is puzzling. Either the distal part of Cu P disappeared completely in Symphyta and the vein in Apocrita is a newly evolved structure or Cu P is suppressed by some genetic mechanism in modern Symphyta. A poorly defined impression in some specimens of *Orussus* (Fig. 1) may be interpreted as Cu P and may hint that the suppressing mechanism was lost early in the evolution of Apocrita (perhaps among ancient Orussoidea?), thus allowing the vein to reappear (i.e. a reversal). Which choice one postulates is of little phylogenetic consequence; both mechanisms result in an apomorphy for Apocrita and the name to be used for the vein might as

well be Cu P in either case because its position and profile fit perfectly into a normal full venation.

Discussion

Ross (1936) uses elements of the two incompatible schemes; the Lameere nomenclature for branches of Media and the discredited Comstock scheme for branches of Cubitus. Therefore Ross's Cu 1 and Cu 2 should be now called Cu A and Cu P.

The vein Cu P is general in putative sistergroups of Hymenoptera and a basal relict is visible in some Symphyta (Xyelidae, Orussidae). An apical part of Cu P may be present as a trace vein in many generalized Apocrita but is absent in Symphyta with the possible exception of Orussidae. Its presence may be due to reversal of a character suppressed in Symphyta and is probably a synapomorphy for Apocrita.

The vein Ross called Cu 1b is probably not a branch of Cu A but most likely is a compound crossvein like the more proximal cu-a, composed of cua-cup and cup-a crossveins inherited from Permian or Triassic ancestors and aligned during the deterioration of Cu P.

My hypothesis is that some Hymenoptera have relicts of Cu P and that there are two cu-a crossveins.

I recommend the following modifications to the Ross system.

Ross 1936	Amendments
Cu	1st Cu A (1Cu)
Cu 1	2nd Cu A (2Cu)
Cu 1a	3rd Cu A (3Cu)
Cu 1b	2 cu-a
cu-a	1 cu-a
Cu 2 in Neoptera	Cu P

For sake of brevity vein Cu A in almost all Hymenoptera might as well be called Cu, just as the putative MA in Hymenoptera universally receives the appellation M. I suggest that the terms Cu A and Cu P could be retained only for forms that have both.

It is unfortunate that the final version of the logical and orderly system of Lameere (1922) (designating all concave veins with the prefix sub-) was never followed, but usage has now firmly fixed remnants of 3 different systems for naming 4 main concave veins: "Subcosta" (Redtenbacher 1886), the only concave vein that he named; "Radial Sector" (Comstock 1895), merely a convenience term to substitute for "R 2+3+4+5"; "Media Posterior" and "Cubitus Posterior" (Lameere 1922, and many earlier papers on the Commentry fossils, and Martynov 1924), 2 concave veins not recognized by Comstock. Other recently used names (empusal, plical) seem to be unnecessary innovations that probably add nothing to an understanding of phylogeny and needlessly complicate nomenclature (Wootton 1979). I agree with Wootton that conservation is a more sensible policy than the coining of new names. Specialists in Hymenoptera using other systems should not lose sight of the strength of Ross's system: the names of veins designate structures believed to be homologous throughout Insecta. Phylogenetic comparisons, even within Hymenoptera, are extremely difficult without such a universal system.

It is not surprising that the spectral distal part of Cu P should escape the notice of researchers dealing with Aculeata s. l. or Ichneumonidae for they rarely need to deal with spectral venation, but the vein is nebulous and plain to see in Rhopalosomatidae. Systems of nomenclature for venation used by most aculeate workers have presumably allowed the phylogenetic significance of a Cu P vein in Rhopalosomatidae to escape attention. Using a traditional naming system, Cu P would be called Brachius or some other term, and homology would be masked by the inadequacies of the traditional nomenclature system.

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SYSTEMATIC NOTES ON SOME BETHYLIDAE FROM BOTSWANA: EPYRINAE (HYMENOPTERA: ACULEATA)

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Abstract.—***Calyozina caperata***, new species, is described from a unique male from Botswana; this is the first record of the genus in Africa. *Epyris breviscapus* Kieffer is transferred to *Trachepyris*, and redescribed from both sexes.

Key Words: Hymenoptera, Bethylidae, *Calyozina*, *Trachepyris*

The present contribution describes two of the more interesting species of Epyrinae collected for the Smithsonian in Malaise traps by Per Forchhammer, Serowe, Botswana. In an earlier paper on several species of Pristocerinae (Krombein 1989) I gave some notes on the ecology of the area where the collections were made.

The abbreviations used in the descriptions are as follows:

LH—length of head from middle of clypeal margin to midpoint of vertex;
WH—width of head including eyes;
WF—width of front (i.e. least interocular distance);
HE—height of eye measured in lateral view;
EV—distance from top of eye to crest of vertex in lateral view;
WOT—width of ocellar triangle including posterior ocelli;
OOL—ocello-ocular line, least distance between posterior ocellus and inner eye margin;
LT—length of thorax, collar excluded, from anterior margin of pronotal disk to posterior end of propodeum.

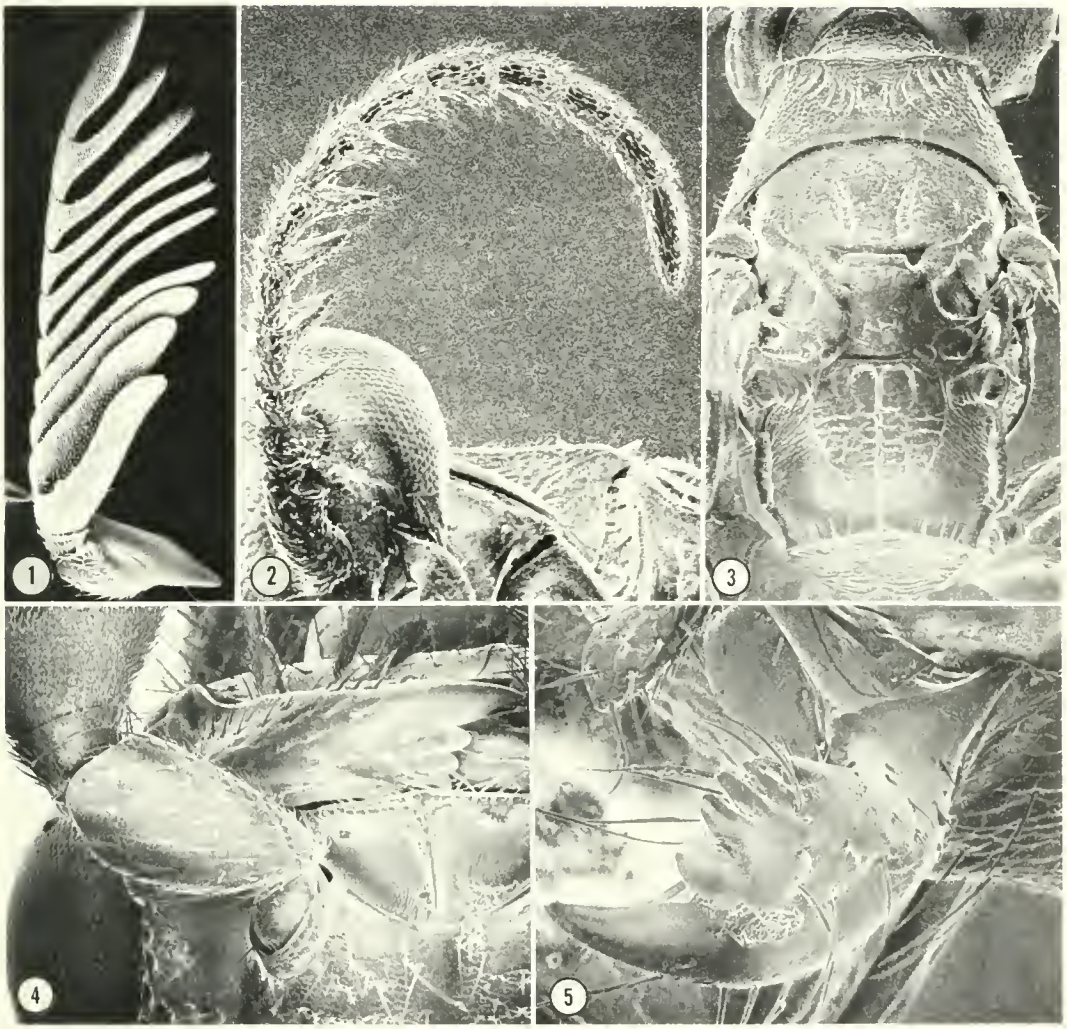
Calyozina caperata Krombein

NEW SPECIES

Figs. 2, 3, 5–8

Male.—Length ca 2.5 mm (terminal abdominal segments estimated, removed before measurement), forewing 1.7 mm. Black, moderately shining, head and thorax finely alutaceous; mandible except teeth, scape, pedicel and first four flagellar segments beneath light red; basal antennal segments above, all of terminal segments, tegula and apical tarsal segments light brown; legs except tarsi darker brown; first four tarsal segments white. Vestiture of head and thorax sparse, short and suberect; flagellar segments above with short, suberect, moderately dense setae, apices of processes on first five flagellar segments with somewhat longer setae. Wings clear, stigma light brown, veins almost colorless.

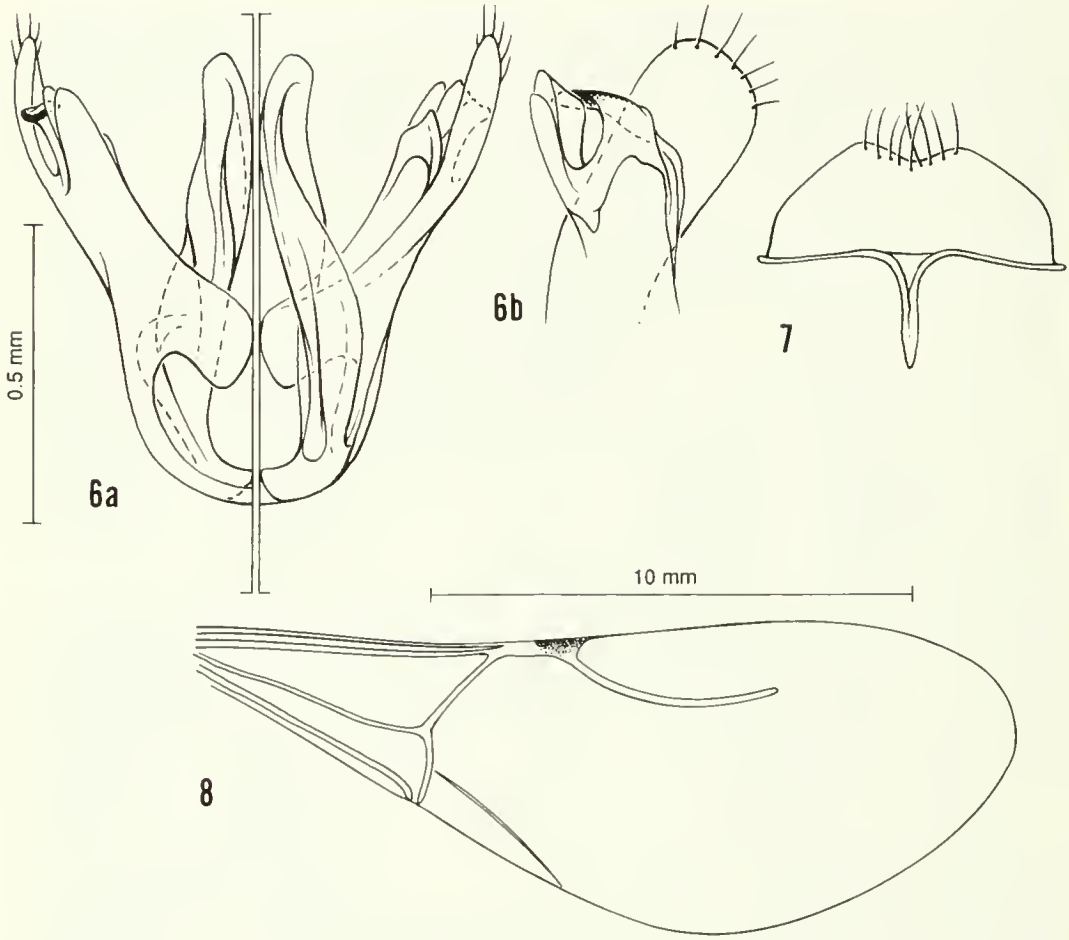
Head: WH 1.09 × LH; WF 1.22 × HE and 0.61 × WH; EV 0.41 × HE; mandible (Fig. 5) stout, not so robust as figured because of foreshortening on micrograph, quinquedentate, apical tooth much longer than inner four; eyes not protuberant, inner orbits diverging slightly above, ocular setae short and quite sparse; front with tiny scat-



Figs. 1–5. Males of *Calyoza staphylinoides* Westwood (?) from Kenya, and *Calyozina caperata* Krombein, holotype from Botswana. 1, Antenna, *C. staphylinoides* (?), 33×; 2, antenna, *C. caperata*, 115×; 3, dorsum of thorax, *C. caperata*, 75×; 4, mandible and base of antenna, *C. staphylinoides* (?), 90×; 5, mandible, *C. caperata*, 455×.

tered punctures and a slight protuberance above each antennal insertion, with a weak carina on each side extending obliquely from protuberance to lower inner eye margin; ocelli in a low triangle, frontal angle about 120°, OOL 0.79 × WOT; vertex broadly rounded; occipital carina complete; antenna 13-segmented (Fig. 2), dorsal length of scape, pedicel and first two flagellar segments in a ratio about 25:12:11:13, first flagellar segment dorsally as long as wide; basal segments modified beneath, in profile pedicel is roundly protuberant beneath, flagellar segments 1–7 have an elongate projection at apex about three-fourths as long as segment on 2–4, somewhat shorter on 1 and 5, very short on 6 and 7, segments 8–11 not modified, subcylindrical, 11 about 1.4× as long as 10.

Dorsum of thorax (Fig. 3), LT 1.8× great-



Figs. 6–8. *Calyozma caperata* Krombein, holotype. 6a, Genitalia, ventral aspect at left, dorsal at right; 6b, lateral aspect, apices of paramere and volsella; 7, subgenital plate; 8, forewing.

est width (at pronotal lobes); pronotal disk with median length a fourth as long as greatest width, lateral fourth strongly carinate anteriorly, middle section a subtriangular raised area, surface adjacent to anterior carina and median raised area with short radiating rugae presenting a wrinkled appearance, disk posteriorly with sparse, scattered, tiny punctures, margin without transverse groove, sides not carinate, rounded to lateral declivous surface; side of pronotum carinate anteriorly on upper half; scutum with scattered tiny punctures, notauli well developed on posterior two-thirds, converging slightly toward apex, parapsidal lines weak, present only on posterior half; scutellum anteriorly with a pair of pits connected by a deep narrow groove; propodeal disk 1.5× as wide as median length, margined laterally by a weakly crenulate groove and carina, posterior margin strongly carinate, posterolateral corner foveolate, median discal carina complete, more strongly sculptured basal area about as long as wide, limiting carinae weak, rounded toward apex, surface with a few weak longitudinal carinae

at base, irregularly and mostly transversely rugulose posteriorly, areas adjacent to basal sculptured section closely, obliquely carinulate, a narrow area anterior to posterior carina with weak, short, longitudinal carinae; posterior propodeal surface lacking a median carina; forewing (Fig. 8).

Abdomen not petiolate; subgenital plate (Fig. 7) short, apical margin weakly emarginate; genitalia (Fig. 6).

Female.—Unknown.

Discussion.—*Calyozina* Enderlein is presently known only from males of six species, the type-species, *ramicornis* Enderlein, from Taiwan, four Neotropical species described by Evans, *amazonica, azurea, mexicana, neotropica*, and *caperata* from Botswana. The included species are similar to males of *Calyoza* Westwood in having pectinate antennae with processes beneath at the apices of many of the flagellar segments (cf Figs. 1, 2). They differ at once from *Calyoza* in having a well-developed first flagellar segment distinctly separated from the second, whereas the first flagellar segment in *Calyoza* is short, broadly joined to the second, forming a ring joint (cf Figs. 2, 4), so that the antennae appear superficially to be only 12-segmented.

The following combination of characters distinguishes *caperata* from its congeners: small size, 2.5 mm long as compared to 5.0–7.0 mm; mandible quinquedentate; pedicel roundly protuberant beneath; pectinations present on flagellar segments 1–7, each shorter than the length of the segment; pronotal disk strongly carinate anterolaterally and with short radiating rugae on median raised area; scutellum anteriorly with lateral pits connected by a deep, narrow groove; and posterior surface of propodeum without a median carina.

Holotype.—♂; Botswana, Serowe, Farmer's Brigade, July 1987, malaise trap, Per Forchhammer (USNM).

Etymology.—From the Latin *caperatus*, wrinkled, in allusion to the distinctive sculpture of the median part of the pronotal disk (Fig. 3).

Trachepyris breviscapus (Kieffer)
NEW COMBINATION
Figs. 9–19

Epyris breviscapus Kieffer, 1904: 402–403; (♂; Cape Verde Islands; holotype in Genoa).—Kieffer, 1908: 27 (listed).—Kieffer, 1914: 333 (redescribed in German).

Acanthepyris spinitarsis Kieffer, 1904: 402 (♀; Portuguese Guinea, now Guinea-Bissau; holotype in Genoa).—Kieffer, 1914: 404 (redescribed in German).

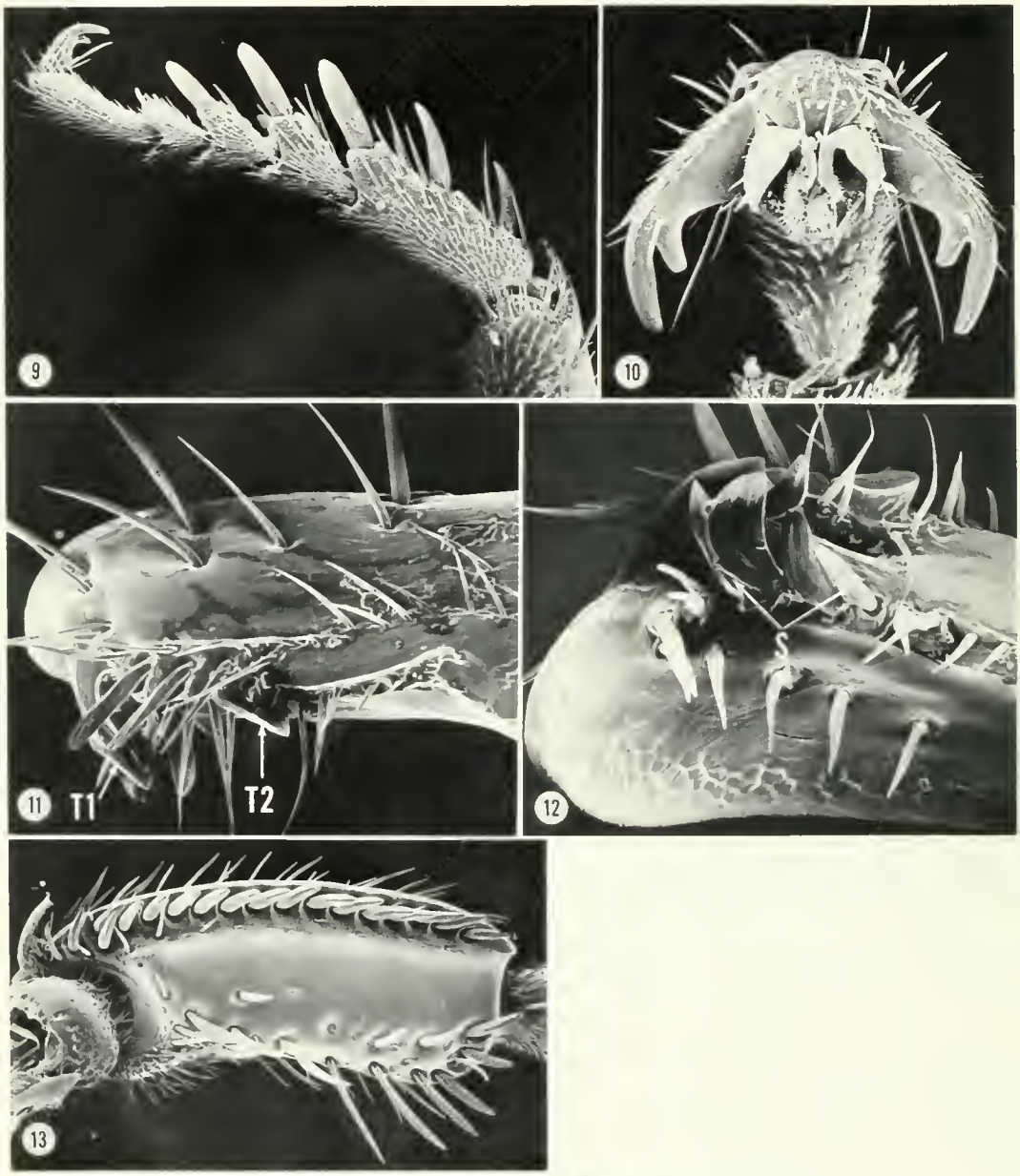
Epyris spinitarsis (Kieffer) Kieffer, 1908: 28 (transferred to *Epyris*).

Acanthepyris propinquus Turner, 1928: 134–135 (♀; Mossel Bay and Queenstown, South Africa; syntypes in London).

Acanthepyris breviscapus (Kieffer) Benoit, 1957: 11 (♂; Zaire; synonymized ♀ *spinitarsis* and ♀ *propinquus*).

This relatively common species of *Trachepyris* occurs from the Cape Verde Islands eastward to eastern Zaire and southward to Botswana and South Africa. Specimens were not available when I prepared a paper on the Ceylonese *Trachepyris* (Krombein 1987), so I take this opportunity to make the generic transfer and a description supplemented by scanning electron micrographs. References in the description, e.g. (Krombein 1987, Fig. 5), contrast the condition in *haemorrhoidalis* (Kieffer) with that in *breviscapus*.

Female.—Length 6.1–8.1 mm, forewing 3.7–4.3 mm. Black, the following light red: mandible except base and inner and outer margins, antenna except apical segments infuscated above, legs variable, mid and hind coxae and rest of all legs light red, or only the tarsi light red, rest of legs light to dark brown, first four abdominal segments black except occasionally apical two-thirds or half of fourth, and all of fifth and sixth segments



Figs. 9–13. *Trachepyris breviscapus* (Kieffer), female. 9, Foretarsus, 85×; 10, foretarsal claws, 215×; 11, mandible, apical half, outer surface, 215×; 12, mandible, apical half, inner surface, 215×; 13, scape, upper surface, 115×.

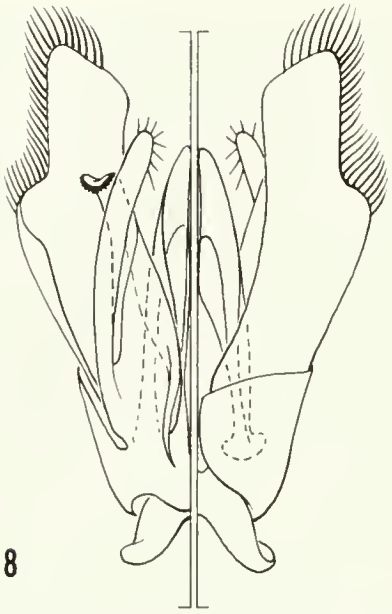
light red. Wings clear to slightly infumated, stigma medium brown, veins lighter brown.

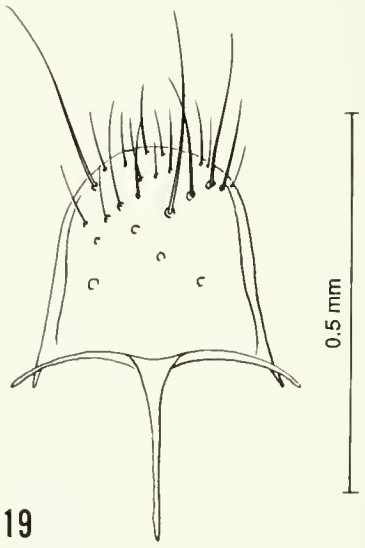
Head shining above, delicately alutaceous, WH 1.20–1.23 × LH, not carinate posterolaterally, posterior margin broadly and slightly incurved; apical half of mandible (dorsal, Fig. 11, ventral, Fig. 12) rounded at apex, inner margin with a long, relatively slender subapical tooth (T1) and a shorter, blunt tooth (T2) somewhat basad,

Figs. 14–17. *Trachepyris breviscapus* (Kieffer), male. 14, Dorsum of thorax, 30×; 15, head and pronotum, 30×; 16, mandible, 150×; 17, antenna, basal segments, 75×.

four modified, flattened sensilla chaetica (S) on ventral surface below subapical tooth; clypeus short, raised along midline but not carinate, apical margin of lobe rounded but with narrow emargination in middle; WF 1.52–1.61 × HE and 0.69–0.71 × WH; front with or without a short, weak median groove anteriorly, usually with small, scattered punctures mostly separated from each other by twice or more a puncture diameter, the punctures rarely somewhat deeper and less separated; scape (Fig. 13) 2.75× as long as wide, longer than in *haemorrhoidalis* (Krombein 1987, Fig. 5), upper surface rather flattened and smooth, margined anteriorly by a row of stout, short bristles that are denser than in *haemorrhoidalis* and posteriorly by sparser, longer bristles; ocelli small, posterior pair almost at hind margin of head, OOL 1.31–1.46 × WOT, front angle of ocellar triangle about 90°.

Thoracic dorsum delicately alutaceous except propodeal disk glossy; pronotum not carinate anteriorly or laterally, impunctate in middle, elsewhere with punctures of moderate size separated by once or twice the diameter of a puncture; scutum and scutellum practically impunctate; dorsal pro-





Figs. 18, 19. *Trachepyris breviscapus* (Kieffer), male. 18, Genitalia, ventral aspect at left, dorsal at right; 19, subgenital plate.

podeal surface 0.57× as long as wide, central area with five longitudinal carinae, the two lateral pairs converging gradually posteriorly, median and lateral carinae reaching margin, intervening pair almost reaching margin, areas between carinae with transverse carinules; posterior surface with complete median carina; forefemur 1.96–2.00× as long as wide, stouter than in *haemorrhoidalis* (2.2× as long as wide); foretarsus (Fig. 9) with pecten about as in *haemorrhoidalis*; tarsal claw cleft (Fig. 10), inner ray shorter than in *haemorrhoidalis* (Krombein 1987, Fig. 8); costa with short setae only, transverse median with short stub.

Male.—Length 4.8–6.1 mm, forewing 3.1–3.6 mm. Coloration almost like that of female except mandibular teeth also dark, legs except coxae usually light red, mid and hind femora infrequently medium brown, and seventh abdominal segment also light red.

Head glossy, in frontal view (Fig. 15), WH 1.08–1.21 × LH, not carinate posterolaterally, posterior margin slightly rounded out; mandible (Fig. 16) quinquedentate, upper and lower teeth longer than three rounded intermediate teeth; clypeus raised along midline but not carinate, apex of median lobe rounded; front with a short, weak, median groove from antennal insertions, punctures small, closer anteriorly and separated by about twice a puncture diameter over most of surface; WF 1.04–1.10 × HE and 0.55 × WH; ocelli in a low triangle, OOL 1.03–1.17 × WOT, front angle of ocellar triangle about 115°; antenna with third segment 1.52–1.55× as long as wide, a bit shorter than fourth (Fig. 17), ratio of first four segments ranging from 20:5:17:20 to 25:5:20:26.

Thoracic dorsum (Fig. 14) glossy; pronotal disk without anterior or lateral carinae, impunctate along a narrow median area, laterally with small punctures separated from each other by one to two puncture diameters; median length of dorsal propodeal surface about half its greatest width, laterally and posteriorly with a crenulate groove adjacent to marginal carina, central area with three to five longitudinal carinae,

the three inner carinae rather close and usually reaching posterior crenulation, lateral pair more separated, often present only anteriorly, curving toward each other when longer but not reaching apex, surface between carinae smooth or with radiating carinules; posterior propodeal surface with complete median carina.

Subgenital plate (Fig. 19); genitalia (Fig. 18).

Remarks.—*T. breviscapus* is rather similar to *haemorrhoidalis* in coloration but is somewhat larger, ♀ 6.1–8.1 mm long compared to 4.7–5.8, ♂ 4.8–6.1 compared to 4.4–4.8, and differs in other details. The female has a relatively longer scape with a row of stout, denser setae anteriorly on upper surface, a stouter forefemur and a shorter inner ray of the tarsal claw. The male genitalia of the two species are quite different, the paramere of *breviscapus* being considerably broader and thinner, and clothed on outer, upper margin with close setae, which are lacking in *haemorrhoidalis* (Krombein 1987, Fig. 19) except for a pair at apex.

Specimens examined (all USNM).—6 ♀, 28 ♂, Botswana, Serowe, Farmer's Brigade, malaise trap, Per Forchhammer, dated as follows: Feb (♀), 18–30 June (♂) and Sep (♂), 1986; Jan (♀), June (♀), Jul (3 ♂), Aug (♀, 2 ♂), Sep (♀, ♂), Oct (♂), Nov (2 ♂) and Dec (♀, 17 ♂), 1987. Dates of collection suggest that seasonal activity begins in June and extends through February.

Acknowledgments

I am grateful to Beth Norden, Department of Entomology, for skillful preparation of uncoated specimens for SEM study, and to Susann Braden, Scanning Electron Microscope Laboratory, for making the micrographs. I thank George Venable, Department of Entomology, for making the line drawings, and for mounting the plates.

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NINTH REPORT ON APHID-HOST RELATIONSHIPS AT THE LOS ANGELES STATE AND COUNTY ARBORETUM (HOMOPTERA: APHIDIDAE)

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Abstract.—This is the ninth report on collections of aphids from plants in the Los Angeles State and County Arboretum at Arcadia, California. Sixteen species are listed with information on their hosts, date of collection, morphs collected, and abundance. This report completes the identification of all material collected by the late Dr. Harry G. Walker, formerly with the Department of Arboreta and Botanic Gardens, Los Angeles State and County Arboretum, Arcadia, California, and submitted to us for identification.

Key Words: aphids, host plants, California

Because aphids are important as plant feeders and vectors of plant viruses, information on their distribution and host plant relationships is of great importance. This is the ninth in a series of papers on the aphids and their host plants in the Los Angeles State and County Arboretum at Arcadia, California. This and four previous papers (Leonard et al. 1972, Leonard and Walker 1973, 1974, Walker et al. 1978) deal with a variety of aphids and their host plants. Four previous papers (Leonard et al. 1970, 1971a, b, c) dealt with six specific aphids and their hosts.

The late Dr. Harry G. Walker, formerly with the Department of Arboreta and Botanic Gardens, Los Angeles State and County Arboretum, Arcadia, California, was responsible for collecting the aphids identified in this paper. The following list includes under each aphid name the host plant, the date of collection, morphs collected, and the relative abundance. This report contains collection information not previously reported and completes the identification of all material collected by Dr. Walker and submitted to us for identification.

The following abbreviations are used for morphs: al = alata, ap = aptera, and ny = nymph.

Aphis craccivora Koch
Amorpha fruticosa L.
28/IV/67 ap, ny Abundant
Artemisia maritima L.
23/V/66 ap, al, ny Abundant
Aphis fabae Scopoli
Nyssa sinensis D. Oliver
31/V/67 ap, ny Moderate
Aphis gossypii Glover
Carya ovata (Mill.) C. Koch
4/V/67 ap Scarce
Gossypium thurberi Tod.
7/VIII/66 al Scarce
Salix babylonica L.
1/V/67 ap, ny Scarce
Aphis spiraecola Patch
Acanthopanax trifoliatus (L.) Voss
20/IV/67 ap, al, ny Moderate
Aloe sp.

28/III/66 al Scarce
Amorpha fruticosa L.
28/IV/67 ap, ny Moderate
Anacampseros telephiastrum DC.
29/III/66 ap, al, ny Abundant
Bauhinia variegata L.
28/IV/67 ap, al, ny Scarce
Buddleia davidii Franch.
25/III/66 al Scarce
Bursaria spinosa Cav.
27/XII/66 ap, al, ny Abundant
Hypericum hookeranum Wight & Arn.
20/IV/67 al Scarce
Lonicera fragrantissima Lindl. & Paxt.
1/II/67 ap, al, ny Scarce
Pittosporum daphniphylloides Hayata
20/XII/66 ap, al, ny Abundant
Prunus lyonii (Eastw.) Sarg.
22/V/66 al, ny Moderate
Rubus palmatus Thunb.
1/VII/66 ap, al, ny Scarce

Aphis sp.
Wisteria floribunda (Willd.) DC.
6/V/67 al Scarce

Aulacorthum solani (Kaltenbach)
Aralia cordata Thunb.
4/V/67 al, ny Scarce
Carya ovata (Mill.) C. Koch
4/V/67 al Scarce
Chrysanthemum 'Rambler'
15/V/67 ap, al, ny Scarce
Liquidambar formosana Hance
6/V/67 al, ny Scarce

Brachycaudus helichrysi (Kaltenbach)
Chrysanthemum 'Rambler'
15/V/67 ap, al Scarce
Gazania linearis (Thunb.) Druce
3/I/67 al Scarce

Cavariella pustula Essig
Salix sp.
1/V/67 ap, ny Scarce

Chaitophorus sp.
Salix babylonica L.
1/V/67 al Scarce

Eulachnus rileyi (Williams)
Hibiscus arnottianus A. Gray kauaiensis
29/X/66 ap, al Scarce

Hysteroneura setariae (Thomas)
Cynodon dactylon (L.) Pers.
27/XII/66 ap, al, ny Abundant

Illinoia sp.
Spiraea longigemmis Maxim.
4/V/67 ap, ny Scarce

Macrosiphum euphorbiae (Thomas)
Anacampseros telephiastrum DC.
29/III/66 al Scarce

Macrosiphum rosae (L.)
Ilex cornuta Lindl. & Paxt.
12/IV/66 ap, al, ny Moderate

Macrosiphum sp.
Gazania linearis (Thunb.) Druce
3/I/67 ap, al, ny Abundant

Myzus persicae (Sulzer)
Anacampseros telephiastrum DC.
29/III/66 ap, al, ny Scarce
Carya ovata (Mill.) C. Koch
4/V/67 al Scarce
Ilex cornuta Lindl. & Paxt.
12/IV/66 al Scarce
Lonicera fragrantissima Lindl. & Paxt.
1/II/67 ap, al, ny Moderate
Lonicera maackii (Rupr.) Maxim.
2/V/67 ny Scarce
Salix babylonica L.
1/V/67 ap, ny Scarce

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NOTE

The Identity of the Genus *Hexaresta* Hering (= *Hyponeothermara* Hardy, n. syn.) (Diptera: Tephritidae)

Hering (1941. Siruna Seva 3: 18) described the monotypic genus *Hexaresta* and its type species *H. juanita* from a single specimen of unknown sex, supposedly from Paramaribo, Surinam. I have examined this specimen, deposited in the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin, through the kindness of Dr. H. Schumann. It is actually the palaeotropical species described by Walker (1859. J. Proc. Linn. Soc. London, Zool. 3: 119) as *Trypeta multistriga*, which is the type species of *Hyponeothemara* Hardy (1986. Pacif. Insects Monog. 42: 71). *Hexaresta* is thus a senior synonym of *Hyponeothermara*, and *juanita* Hering is a junior synonym of *Hexaresta multistriga* (Walker), n. comb.

The holotype of *juanita* is in poor condition, with its thorax broken and its abdomen, most thoracic setae, left foreleg and right hindleg missing. Despite this, it can be clearly recognized as a specimen of *multistriga* because of Hardy's (1986) thorough redescription of the latter. I have also compared the type with a female from New Guinea in the National Museum of Natural History collection which Hardy determined as *multistriga*. The *juanita* type easily runs to *Hyponeothermara* in the key to the genera of Acanthonevrina in Hardy (1986); most of the diagnostic characters in the key, including the shape of the facial carina and the nonsetulose scutellum, can be observed on the *juanita* holotype. Although the thorax is broken, the mesonotal color pattern, which is distinctive of *multistriga*, is also evident in the *juanita* holotype. It differs only slightly from the pattern in Hardy's fig. 44c and that of the female examined; the presutural dark brown spots are slightly larger and the postsutural spots are fused at the dorsocentral setae. The color of the head agrees closely with Hardy's description; there is no frontal vitta as in *Hexaresta formosa* (Malloch), n. comb., the only other species that Hardy (1986) placed in *Hyponeothemara*. The wings are in good condition and their pattern is almost identical to that of the specimen examined, differing only by the lack of the small marginal hyaline spot between the two large hyaline spots in cell r_1 (compare also fig. 15 of Hering (1941) with fig. 44d of Hardy (1986)). Hardy (1986) states that this spot is variable in *multistriga*. Hering's figure is erroneous in showing the base of cell c dark; it is subhyaline in the *juanita* holotype like most of the rest of the cell.

Hexaresta multistriga almost certainly is not native to the Neotropical Region. Hardy (1986) reported its distribution to be Sulawesi, the Moluccas, and New Guinea, and species that he considered closely related, such as *Hexaresta formosa* and the species of *Neothemara* Malloch and *Pseudoneothemara* Hardy, also occur in the Oriental and Australasian Regions. No closely related species are known from the New World. Hering (1941) accurately recorded the data on the label of the holotype of *juanita*, which reads "S. Amerika, Surinam, 5.08, Bezirk [district of] Paramaribo, C. Heller S. V." These data are doubtful, however, unless this species has been introduced into Surinam. More likely, considering the poor condition of the *juanita* holotype, is that it was placed on its present pin after falling off a different one.

I am grateful to A. Freidberg (Tel Aviv Univ.), D. E. Hardy (Univ. of Hawaii), and D. A. Nickle and N. E. Woodley (Systematic

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MORPHOLOGICAL VARIATIONS IN THE HEMELYTRA OF *CRYPHOCRICOS HUNGERFORDI* USINGER (HETEROPTERA: NAUCORIDAE)

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Abstract.—Morphological variations in the hemelytra of *Cryphocricos hungerfordi* Usinger are described and illustrated. The distal margins of hemelytra of brachypterous forms are highly variable and may be straight, concave, convex, and asymmetrical. Additionally, a submacropterous form, intermediate between the brachypterous and macropterous forms, is described and illustrated. The northeasternmost record of the distribution of *C. hungerfordi* is now the South Llano River in central Texas.

Key Words: Insecta, creeping water bug, polymorphism, wing

The Naucoridae, or creeping water bugs, consists of predacious, aquatic bugs that primarily are pantropical in distribution. These bugs are common components of both lotic and lentic faunas.

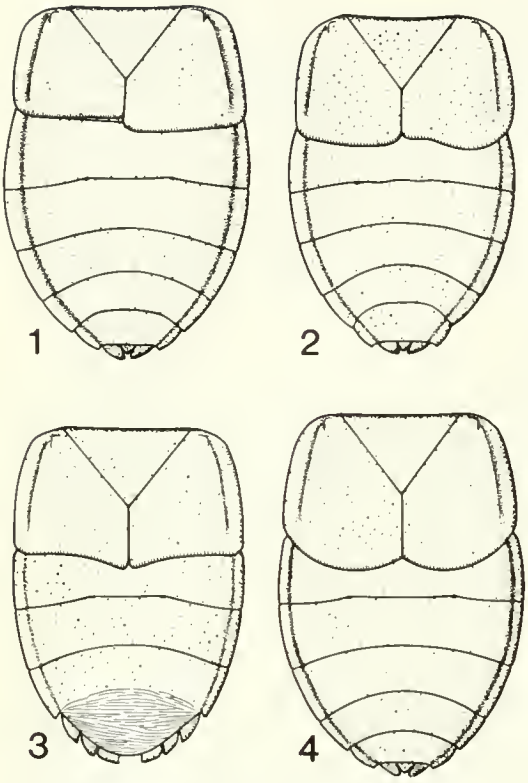
The genus *Cryphocricos* is restricted to the New World and La Rivers (1971, 1974, 1976) listed 14 species. Members of the genus are strongly dimorphic in thoracic development (Parsons 1974) which is associated with the brachypterous and macropterous conditions (Usinger 1941, 1947). The brachypterous form is more common than the macropterous form (Usinger 1941), and Parsons & Hewson (1974) considered macropters very rare.

The only member of this genus known to occur in the United States is *Cryphocricos hungerfordi* Usinger. The range of this species is from Mexico north to central Texas. Thus far, in the U.S. it has been recorded from only the Frio, Nueces, and Pecos Rivers in Texas (Polhemus & Polhemus 1988). Usinger (1947) described this species from both brachypterous and macropterous forms, and the type specimen is brachypterous. Usinger (1947) used the morphological condition of hemelytra in three of eight couplets in his key to the species of brachypterous forms of *Cryphocricos*.

Variations in hemleytral morphology of brachypterous *C. hungerfordi* are presented herein, and a third morphotype is described and illustrated. Additionally, the northeasternmost known limit of the range of *C. hungerfordi* is extended to the South Llano River in central Texas. Voucher specimens of each morphotype and the extremes of variation in the brachypterous condition are deposited in the Texas Tech University Entomological Collection.

STUDY SITE

A total of 790 adults of *C. hungerfordi* was collected from a single population in the South Llano River on the Texas Tech University Center campus in Junction, Kimble Co., Texas, from April 1988 through January 1989. The South Llano River is on the Edwards Plateau and is north of the Balcones Fault Zone. This locality is ca. 160–250 km north and northeast of the previous



Figs. 1–4. Morphological variations in the hemelytra of brachypterous *Cryphocricos hungerfordi*.

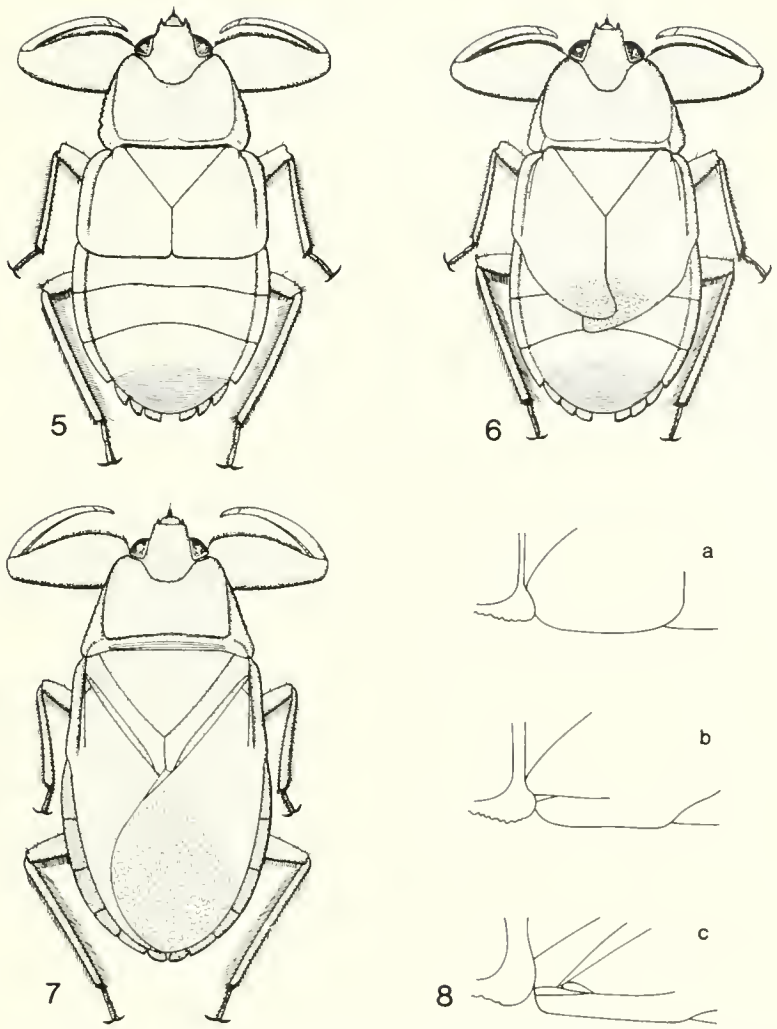
records of *C. hungerfordi*, which were in the vicinity of the Balcones Fault Zone (Polhemus & Polhemus 1988) and represents the northeasternmost known limit of the range of this species.

Morphological Variations in Hemelytra

Asymmetry.—Asymmetry in the hemelytra is common in the brachypterous forms. Specimens preserved in alcohol were examined and illustrated prior to pinning; thus, the asymmetry is not an artifact of pinning. Generally, asymmetry is evidenced as one wing shorter than the other (Fig. 1). This was apparent in many specimens with straight distal margins. Additionally, asymmetry was noted as hemelytra of different shapes (e.g. one straight and one sinuate distal margin [Fig. 2]). The illustration of the brachypterous male in the original description (Usinger 1947) appears to approach this condition. Whether this was intentional or an imperfection in drawing is not known, as there is no mention of asymmetry in the text.

Brachyptery.—Symmetrical morphological variations in the hemelytra of brachypterous specimens are continuous, rather than falling into discrete categories of variation described here. The distal margins may be concave with the posteromedial corners produced (Fig. 3). In addition to the concavity, the angle of the distal margins may slope caudad toward the midline. A second variation is that of highly rounded distal margins (Fig. 4). Curvature is continuous from the posteromedial corners and the distal margins merge with the costal margins. The posterolateral corners generally are poorly defined. The form that typically is described in keys (e.g. Polhemus 1984) has truncate, squared-off hemelytra (Fig. 5). Illustrations in the original description (Usinger 1947) showed the female to have straight distal margins of the hemelytra.

Submacroptery.—In addition to the variable brachypterous forms and macropterous form (Fig. 7), a submacropterous form exists (Fig. 6). Usage of the term submacropterous is consistent with terms proposed by Slater (1975) to classify the major types of hemelytral structure. In this condition the wings extend to the 5th abdominal tergum and are represented by both corium and membrane, whereas membrane is absent in the brachypterous form. The hemelytral apices are produced and overlap. The percentage of each hemelytron represented by the embolar area (14.0), measured at the level of the apex of the scutellum, is intermediate between that of the wider brachypterous (14.9 ± 0.2 [$\bar{y} \pm$ SE]) and narrower macropterous (11.5 ± 0.9) forms. The posterior margin of the pronotum and the humeral region of each hemelytron, including the embolar suture, are intermediate in degree of development as compared with bra-



Figs. 5–8. 5–7, Brachypterous, submacropterous, and macropterous morphotypes, respectively, of *Cryphocricos hungerfordi*. 8, Dorsolateral view of humeral angle of left hemelytron in brachypterous (a), submacropterous (b), and macropterous (c) morphotypes of *Cryphocricos hungerfordi*. Note intermediate level of development of sutures and pronotum of submacropterous form.

chypterous and macropterous forms (Fig. 8). Because only one male submacropterous specimen was collected, it was not dissected to examine the extent of intermediate conditions of the thorax and for presence of hindwings.

Discussion

A total of 790 adults was collected in the South Llano River; six were macropterous (0.8%) and one was submacropterous (0.1%). The remainder (783 specimens) were brachypterous. With the discovery of the submacropterous form, this species should be referred to as polymorphic rather than dimorphic.

Lindroth (1949) concluded that for certain carabids, environmental uncertainty favors alary dimorphism, but in a stable environment brachyptery predominates.

Additionally, Slater (1972) suggested that the proportion of species with alary polymorphism may not only indicate ecological stability of that area, but also stability in terms of evolutionary time. The South Llano River is a stable environment for naucorids (water temperature no colder than 11.5°C during the winter and a constant abundance of prey). Therefore, because the brachypterous form is predominant and the macropterous form is present at such a low frequency, it is unknown whether the submacropterous form is aberrant or a consistent morphotype at a very low frequency of occurrence.

Despite the diverse variations in the brachypterous condition, *C. hungerfordi* still may be identified with the key prepared by Usinger (1947). However, if this kind of variation is present in brachypterous forms of *C. barozzii* Signoret, *C. breddini* Montandon, *C. peruvianus* De Carlo, or *C. rufus* De Carlo, many specimens cannot be identified properly with the key because couplet six uses the shape of the "apical margins of hemelytra." Studies on populations of those species are needed to determine the extent of this morphological variation.

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TAXONOMIC NOTES ON SOME NORTH AMERICAN APHIDS

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Abstract.—Typic material of four poorly known aphid species from North America, *Amphorophora singularis* Hottes & Frison, *Capitophorus corambus* Hottes & Frison, *Phorodon scrophulariae* Thomas and *Kakimia mimulicola* Drews & Sampson, has been examined. Appropriate synonymy or generic placement is suggested for each species.

Key Words: Homoptera, Aphididae, taxonomy, North America

There are nominal aphid species in the fauna of every region that have been described from one or a few specimens and have rarely, if ever, been identified after the initial collection. The reasons for this vary, but possibly the most common reason is that the original generic placement, based on earlier generic concepts and often erroneous host records, is wrong. The four species discussed below fall into this category, and the synonymy or appropriate generic placement for each is given. For each of the cases below, careful comparisons were made between the typic material and specimens of the species to which we believe they belong. Measurements and photographs taken from the typic material are provided to support the placement. The quality of these photographs varies with the condition of the specimen on the slide. No attempt was made to remount the type specimens.

Amphorophora singularis Hottes and Frison (1931) was described from a single aptera, taken on an unknown species of grass in Golconda, Illinois. We cannot distinguish it from *Microparsus* (*Megouroparsus*) *kislankoi* Smith & Heie 1963, for which we believe it is an earlier name. Characters of *A. singularis* fit those of the subgenus *Megouroparsus* and match those in the original description of *kislankoi*. Most obvious are the distinct sclerotization pattern, shape of siphunculi, diverging antennal tubercles, short setae on body, head, antennae and legs, and spinules on frontal tubercles and femora. Measurements taken from the type specimen (Table 1) closely match those from the type series of *M. kislankoi* as does the photograph of the holotype of *A. singularis* (Fig. 1) when compared to the photograph of *M. kislankoi* in the original description (Smith & Heie 1963). We therefore consider *Microparsus* (*Megouroparsus*) *kislankoi* Smith & Heie a synonym of *Microparsus* (*Megouroparsus*) *singularis* (Hottes & Frison). *M. kislankoi* is reported to have as its hosts several species of *Lespedeza* (Leguminosae). It is possible that the single aptera of *singularis* was only accidentally on the grass.

Capitophorus corambus Hottes and Frison, 1931 was described from an alata (the holotype), one aptera (labelled morphotype) and one alata (paratype) collected from *Rosa* sp. in Galena, Illinois. The very slightly swollen siphunculi, sensoria only on antennal segment III in both aptera and alatae,

Fig. 1. Holotype of *Amphorophora singularis* on slide #10381, INHS (7.8×).

slightly capitate setae on head and body and shape of head and cauda indicate that they are the *Ribes* feeding species *Hyperomyzus* (*Neonasonovia*) *ribiella* (Davis 1919). Other specimens on the slides are one aptera without antennae which is *Rhodobium porosum* (Sanderson) and one nymph of *Chaetosiphon* (*Pentatrichopus*) sp.? supporting the recorded host as rose. Photographs of the holotype and morphotype of *C. corambus* are shown in Figs. 2 and 3 and measurements are given in Table 1. We therefore

Fig. 2. Holotype of *Capitophorus corambus* on slide #10657, INHS (7.8×).

Fig. 3. Morphotype of *Capitophorus corambus* on slide #10658, INHS (6.25×).

consider *Capitophorus corambus* Hottes & Frison a synonym of *Hyperomyzus* (*Neonasonovia*) *ribiella* (Davis).

A slide labelled *Myzus scrophulariae* bears the single specimen taken on *Scrophularia nodosa* at Carbondale, Illinois, and described as *Phorodon scrophulariae* Thomas 1879. Characters such as converging, rugose frontal tubercles, swollen and imbricated siphunculi and strongly wrinkled abdominal dorsum place this specimen in the genus *Hyalomyzus*. We believe it is the species described as *Rhopalosiphum monardae* Davis 1911, now known a *Hyalomyzus monar-*

Fig. 4. Lectotype of *Phorodon scrophulariae* on slide #2798, INHS (6.25×).

Fig. 5. Cotype of *Kakimia mimulicola*, slide from Essig Collection at U.C. Berkeley (6.25×).

dae (Davis) and for which it would be an older name. We think it is undesirable to replace a well known and appropriate name with a previously unrecognised and inappropriate name and will request the International Commision on Zoological Nomenclature to supress the name *scrophulariae*.

A photograph of the lectotype of *Phorodon scrophulariae* is shown in Fig. 4, measurements are given in Table 1.

Kakimia mimulicola Drews and Sampson 1937 was described from *Mimulus* sp. (Scrophulariaceae). The short, distinctly shaped cauda, W-shaped front and rhinarial

Fig. 6. Cotype of *Kakimia mimulicola*, slide from Essig Collection at U.C. Berkeley (6.25×).

Table 1. Measurements taken from holotype, lectotype or cotype specimens of species mentioned above, all measurements are in millimeters. Abbreviations are as follows: Ant. = antennal segment, Ant. VIb = base of sixth antennal segment, Ant. VIpt = process terminalis of sixth antennal segment, URS = ultimate rostral segment, Ht II = second segment of hind tarsus, Set. URS = accessory setae on ultimate rostral segment, Set. Cauda = setae on cauda, n.m. = not measurable.

Species Name	Body	Siphunculi	Cauda	Antennal Segment					Second Hind Tarsus	Ultimate Rostral Segment		Caudal Setae
				III	IV	V	VIb	VIpt		Length	# of Setae	
Amphorophora singularis Hottes & Frison												
Holotype, aptera	1.71	0.43	n.m.	0.54	0.53	0.45	0.15	0.92	n.m.	0.1	2	2
Capitophorus corambus Hottes & Frison												
Holotype, alata	1.26	0.47	0.2	0.59	0.38	0.33	0.095	0.77	0.1	0.14	5	8
Morphotype, aptera	1.47	0.57	0.27	0.57	0.31	0.3	0.097	n.m.	0.1	0.15	8	7
Phorodon scrophulariae Thomas												
Lectotype, aptera	1.56	0.35	n.m.	0.42	0.3	0.26	0.12	0.41	0.1	0.12	1	4
Kakimia mimulicola Drews & Sampson												
Cotype, alata	1.6	0.27	0.1	0.39	0.25	0.20	0.12	0.32	0.09	0.13	2	6
Cotype, aptera	1.98	0.35	0.12	0.29	0.19	0.14	0.12	0.28	0.08	0.14	2	4

distribution in alatae suggest it belongs in the genus *Myzodium*. No clear differences can be found between it and either *Myzodium modestum* (Hottes) 1926 or *Myzodium knowltoni* Smith and Robinson 1975 both of which have as their hosts a moss (Bryophyta). It is regarded here as *Myzodium mimulicola* (Drews & Sampson), but its separate identity requires experimental confirmation. Photographs of an alata and aptera taken from cotype slides are shown in Figs. 5 and 6 and measurements are given in Table 1.

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SEASONAL EMERGENCE PATTERNS AND DIVERSITY OF PLECOPTERA ON BIG HUNTING CREEK, MARYLAND, WITH A CHECKLIST OF THE STONEFLIES OF MARYLAND

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Abstract.—Species diversity and prevalence patterns of adult stoneflies were studied on Big Hunting Creek, Maryland, primarily by adult sampling. Twenty-two genera represented by 39 species emerged throughout the year. The greatest number of species occurred from April through June. Seventeen of the species were recovered from stomach pump samples of trout from Big Hunting Creek. Twenty-five of the species are new records for the state of Maryland. An updated list of the stoneflies of Maryland is provided.

Key Words: Plecoptera, stonefly, species list

This study summarizes four years of adult stonefly collections on Big Hunting Creek, Maryland, situated within the boundaries of Catoctin Mountain Park and Cunningham Falls State Park. Included in our data are specimens obtained from stomach pump samples from trout caught in Big Hunting Creek and donated by local fishermen. Since a number of the species of stoneflies are new records for the state, an updated list of the Plecoptera of Maryland is given.

Although a number of recent stonefly surveys have been conducted on streams in North America, none has been reported for Maryland. Investigations on eastern streams include those of Harper and Magnin (1969) [Quebec], Harper and Pilon (1970) [Quebec], Woodall and Wallace (1972) [North Carolina], White (1974) [Kentucky], Neves (1978) [Massachusetts], Tkac and Foote (1978) [Ohio], Stark (1980) [South Carolina], Masteller (1983) [Pennsylvania], and Singh et al. (1984) [Ontario]. Plecoptera diversity studies on mid-western and western streams include those of Sheldon and Jewett (1967) [California], Radford and Hartland-Rowe (1971) [Manitoba], Narf and Hilsenhoff (1974) [Wisconsin], Kerst and Anderson (1974) [Oregon], Ellis (1975) [Alaska], and Friesen et al. (1984) [Manitoba].

This investigation is part of a larger long-term documentation of the insect fauna of relatively unpolluted Big Hunting Creek. Specific aquatic species can be used as indicators of water quality (Hynes 1970). Hence, it is important to know not only which species are present in the stream, but also to understand the sequence in which they emerge, their life histories, and their ecological requirements. As stream characteristics change due to the encroachment of man, so do the components of benthic communities. Species data bases thus become important to document stream changes.

Study Area

Big Hunting Creek (39°37′N, 77°27′W) originates in the Catoctin Mountains in

western Frederick County, Maryland, and runs into the Monocacy River. This general area of Frederick County receives 76–102 cm of rain per year with approximately 102 cm of snow in the winter. The stream is bordered by Catoctin Mountain Park to the north and Cunningham Falls State Park to the south. In Cunningham Falls State Park the stream flows into and out of the 17.4 hectare Cunningham Lake. Minimum flow from the lake in the late summer and fall is reported to be 0.045 m^3. During the winter months the stream occasionally freezes over (Frederick County Planning and Zoning Commission 1969).

The stream bed is composed of a range of particle sizes from small rocks and gravel to medium size boulders. Several sections of the stream bed exhibit bedrock outcrops. There are approximately 22 different genera of trees represented in both Catoctin Mountain Park and Cunningham Falls State Park (Buchart and Horn Consulting Engineers and Planners 1964). Dominant species of the drainage basin include those in *Quercus* (oak), *Carya* (hickory), *Acer* (maple), and *Liriodendron* (poplar). The majority of the trees are second and third growth hardwoods averaging 20–30 cm in diameter.

Materials and Methods

The field work was carried out on Big Hunting Creek over a four year period from February, 1984, through September, 1988. The data are based primarily on adult specimens. Most of the collecting was in the areas adjoining the stream between the eastern entrance of Catoctin Mountain Park on Maryland Route 77 and Hunting Creek Lake and above Cunningham Falls to the west entrance of Catoctin Mountain Park. Within the study area, several intermittent streams run into Big Hunting Creek. No effort was made to collect along these feeder streams. Many of the specimens were hand collected at the Camp Pineil Bridge on Maryland Route 77. Additional material was collected along the edges of the stream on rocks as well as on vegetation. Several of the smaller species were collected using a mouth-operated aspirator.

Specimens were also obtained from stomach samples of either rainbow or brown trout caught in the study area of Big Hunting Creek and provided by local fishermen. The stomach pump consists of a tube approximately 0.8 cm (O.D.) by 20 cm with a rubber squeeze bulb attached to the end. To obtain a sample of the stomach contents, the tube was placed into the mouth of the trout and gently forced down the esophagus. After insertion, a small volume of water (1 ml depending upon the size of the fish) was slowly released into the trout's stomach and drawn back up into the stomach pump. The stomach pump was then withdrawn and the fish released unharmed. As a general rule fish under 25–28 cm were not pumped. The sample was then placed in a vial, the water poured off and 70% ethanol added.

All collected material was preserved in 70% ethanol. Each sample was labelled with collection data and an accession number. The material studied was stored in the authors' collections, either in the Department of Zoology at Howard University or in the Department of Biology at the University of Tennessee at Chattanooga. Representative material has been deposited at Catoctin Mountain Park.

Results and Discussion

Figure 1 lists the species of stoneflies and the time periods during which adults were collected. A total of 4286 specimens were collected during the course of the study. The number of specimens identified as well as the number of different collections for each species are also listed. The latter usually represented different collecting dates but occasionally, if separate collections were made in different sections of the park on the same date, they were labelled as separate collections.

Altogether thirty-nine species were collected, representing 22 genera. Adults oc-

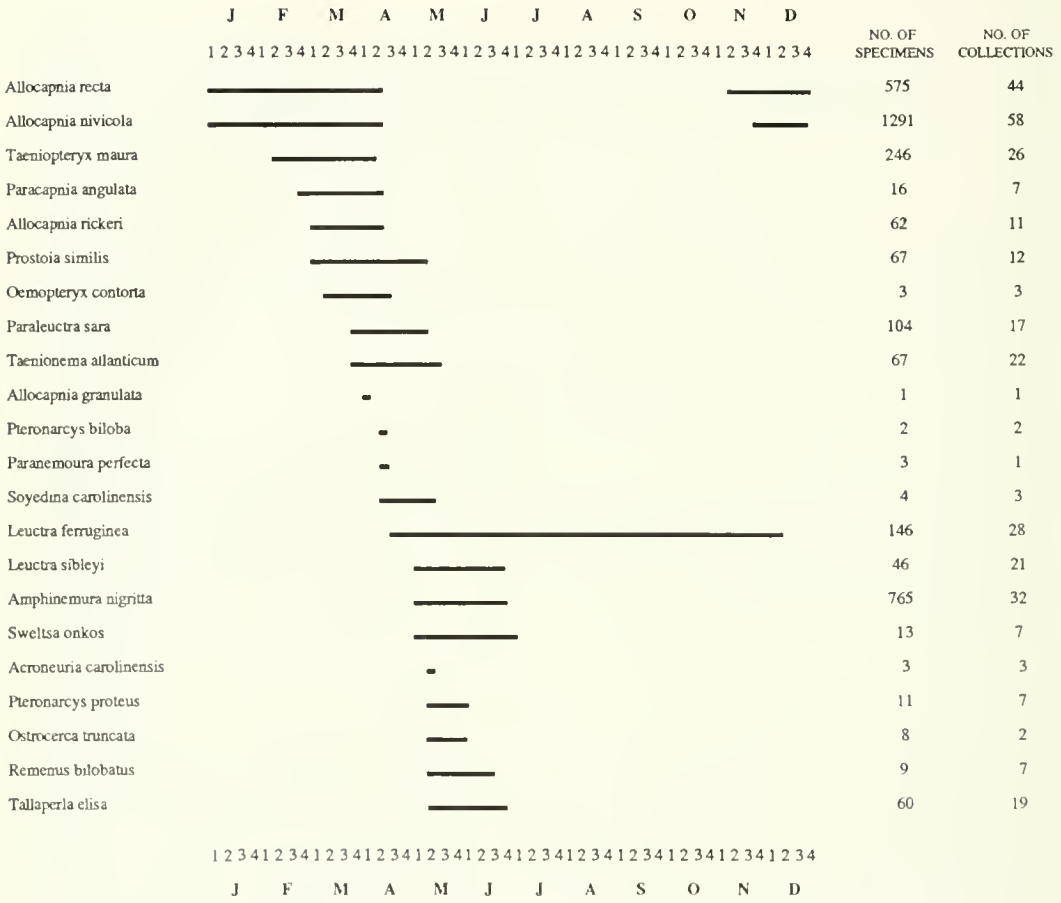


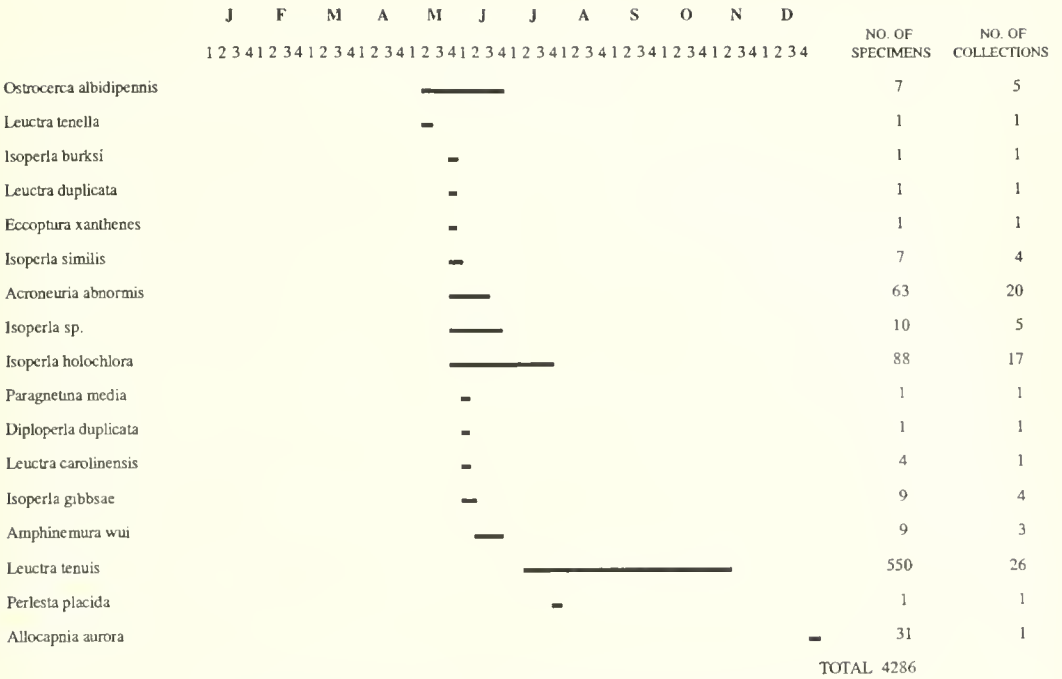
Fig. 1. Inclusive collection dates for adult stoneflies based on collections from February 1984 to September 1988.

curred during every month of the year, but the majority of species were collected from April through June.

Several genera were represented by more than one species, including *Leuctra* (six), *Allocapnia* and *Isoperla* (five), *Acroneuria, Amphinemura, Ostrocerca,* and *Pteronarcys* (2). Fifteen genera were each represented by one species, eight of those being represented by a single specimen.

The five most abundant species in descending order were *Allocapnia nivicola* (Fitch) [1291], *Amphinemura nigritta* (Provancher) [765], *Allocapnia recta* (Claassen) [575], *Leuctra tenuis* Pictet [550], and *Taeniopteryx maura* (Pictet) [246]. These five species represented 80% of all the material collected. The most abundant species collected, *A. nivicola,* represented approximately one-third of all the material collected. Three of the five most abundant species emerged in the winter or early spring and were present for long periods. This may account for the larger number of specimens collected.

Several species represented by multiple collections over several months and by large numbers of individuals indicated that males were present in greater numbers than females at the beginning of the emergence period. Species exhibiting this pattern include *Allocapnia nivicola, A. recta* and *A. rickeri.* Table 1 lists the ten earliest collections for *A. nivicola.* Chi-square analysis using the



	1 2 3 4 J	1 2 3 4 F	1 2 3 4 M	1 2 3 4 A	1 2 3 4 M	1 2 3 4 J	1 2 3 4 J	1 2 3 4 A	1 2 3 4 S	1 2 3 4 O	1 2 3 4 N	1 2 3 4 D
Species Beginning Emergence	0	2	5	5	17	5	2	0	0	0	2	1
Total Species	2	4	9	14	22	17	5	2	2	2	4	4
Total New Emergences	0	2	7	12	29	34	36	36	36	36	38	39

total number from these collections indicates a significant deviation from the expected 1:1 ratio of males to females ($P = 0.0001$). Slightly earlier male emergence patterns for adult stoneflies have been reported by a number of workers including Brink (1949), Sheldon and Jewett (1967), Harper and Pilon (1970), Nebeker (1971), Neves (1978) and Masteller (1983). In contrast, other species in our study also represented by multiple collections and large individual numbers did not show a dominance of males at the beginning of the emergence period. These included *Leuctra ferruginea, L. tenuis, Amphinemura nigritta* and *Taeniopteryx maura.*

Seventeen species were obtained from approximately forty separate stomach pump samples. Two species, *Allocapnia granulata* and *Paranemoura perfecta,* were added to the species list based on specimens obtained solely from this sampling technique. *Allocapnia granulata* was represented by a single specimen and *P. perfecta* was represented by four specimens (2 males, 1 female, and 1 nymph). Stomach pump samples also provided a major portion of the specimens for two additional species, *Soyedina carolinensis* and *Oemopteryx contorta.* Of the four adult specimens recorded for *S. carolinensis,* two stomach pump samples each provided a single adult specimen. Of the twelve specimens recorded for *O. contorta,* three adults were collected by hand and a total of nine nymphs were recovered from three separate stomach pump samples. An in depth presentation of the stomach pump data is being published separately.

There are a number of variables which must be considered when making conclu-

Table 1. Partial collection data for *Allocapnia nivicola*: The ten earliest collections.

Date	Males	Females
Nov. 22, 1984	2	—
Nov. 24, 1984	7	1
Nov. 30, 1984	11	1
Dec. 9, 1984	13	3
Dec. 26, 1986	2	1
Dec. 8, 1987	3	—
Dec. 13, 1987	6	—
Dec. 24, 1987	1	—
Dec. 24, 1987	41	19
Dec. 24, 1987	5	—
Totals	76	25

sions about emergence based on adult collections. The total number of specimens collected is not necessarily a correct indication of the abundance of a particular species in the stream. Some species emerge by crawling out of the water on rocks, others fly directly off the surface of the water to resting spots in the tops of trees. Secondly, the adults of some species are available for several days to a week while others are available for several months.

Harper and Pilon (1970) report two types of emergence patterns: a short synchronous period where 90% of the population emerges within several days, and an extended emergence where 50% of the population emerges half way through the emergence period. *Allocapnia nivicola* and *Leuctra ferruginea* are examples of species with extended emergences. Due to this long period of adult availability, specimens are collected more frequently when making random collections.

The periods that adults are present for those species with extended emergence periods should not be misinterpreted. The greater longevity of females over males has been reported by Nebeker (1971), Finni (1975) and Lillehammer (1975). Although adult specimens were being collected, the actual emergence of adults may well have been completed. Thus, adult emergence period should not be confused with adult life span or adult duration. The data reported in Fig. 1 represents initial emergence dates and reports the duration that adults were detected in the vicinity of the stream.

Stark et al. (1986) reported 33 species of Plecoptera from Maryland. During this study we collected an additional 25 new state records which are indicated by an * in the updated list of 58 species that follows.

Order Plecoptera
Suborder Arctoperlaria
Group Euholognatha
Superfamily Nemouroidea
Family Taeniopterygidae
Subfamily Taeniopteryginae

Taeniopteryx burksi Ricker and Ross
T. lonicera Ricker and Ross
T. maura (Pictet)

Subfamily Brachypterinae

**Oemopteryx contorta* (Needham and Claassen)
Taenionema atlanticum Ricker and Ross

Family Nemouridae
Subfamily Amphinemurinae

**Amphinemura nigritta* (Provancher)
**A. wui* (Claassen)

Subfamily Nemourinae

**Ostrocerca albidipennis* (Walker)
O. truncata (Claassen)
**Paranemoura perfecta* (Walker)
**Prostoia similis* (Hayen)
Shipsa rotunda (Claassen)
**Soyedina carolinensis* (Claassen)

Family Leuctridae
Subfamily Leuctrinae

**Leuctra carolinensis* Claassen
**L. duplicata* Claassen
**L. ferruginea* Walker
L. sibleyi Claassen
**L. tenella* Provancher
**L. tenuis* Pictet
**Paraleuctra sara* (Claassen)

Family Capniidae

Allocapnia aurora Ricker
A. curiosa Frison
A. granulata (Claassen)
A. maria Hanson
A. nivicola (Fitch)
A. pygmaea (Burmeister)
A. recta (Claassen)
A. rickeri Frison
A. vivipara (Claassen)
A. wrayi Ross
Paracapnia angulata Hanson

Group Systellognatha
Superfamily Pteronarcyoidea
Family Pteronarcyidae

**Pteronarcys biloba* Newman
**P. proteus* Newman

Superfamily Peltoperloidea
Family Peltoperlidae
Subfamily Peltoperlinae

**Tallaperla elisa* Stark
T. maria (Needham and Smith)

Superfamily Perloidea
Family Perlodidae
Subfamily Isoperlinae

Clioperla clio (Newman)
**Isoperla burksi* Frison
**I. gibbsae* Harper
I. holochlora (Klapalek)
I. similis (Hagen)

Subfamily Perlodinae

**Diploperla duplicata* (Banks)
Isogenoides hansoni (Ricker)
**Remenus bilobatus* (Needham and Claassen)

Family Perlidae
Subfamily Acroneurinae

Acroneuria abnormis (Newman)
A. arenosa (Pictet)
**A. carolinensis* (Banks)
A. filicis Frison
Attaneuria ruralis (Hagen)
Eccoptura xanthenes (Newman)
**Perlesta placida* (Hagen) 'complex'
Perlinella drymo (Newman)
P. ephyre (Newman)

Subfamily Perlinae

Agnetina annulipes Stark
A. flavescens (Walsh)
**Paragnetina media* (Walker)

Family Chloroperlidae
Subfamily Chloroperlinae

Alloperla atlantica Baumann
Haploperla brevis (Banks)
**Sweltsa onkos* (Ricker)

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NEW SPECIES OF PREDACEOUS MIDGES OF THE TRIBE CERATOPOGONINI FROM SUBANTARCTIC ARGENTINA (DIPTERA: CERATOPOGONIDAE)

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Abstract.—Four new species of predaceous midges of the tribe Ceratopogonini from subantarctic Argentina are described and illustrated: ***Diaphanobezzia patagonica***, ***Macrurohelea fuscipennis***, ***M. similis***, *and* ***Notiohelea pilosa***. A key to the Neotropical species of *Macrurohelea* is presented.

Key Words: Diptera, Ceratopogonidae, Ceratopogonini, Neotropical, subantarctic, Argentina, predaceous midges

Wirth and Grogan (1988) listed five genera of predaceous midges of the tribe Ceratopogonini whose distributions are exclusively subantarctic or nearly so: *Austrohelea* Wirth and Grogan, with 7 species, 6 are from Australia, Campbell Island, New Zealand and Tasmania, and one species from southern Argentina; *Diaphanobezzia* Ingram and Macfie, with 2 species from Argentina; *Isthmohelea* Ingram and Macfie, with one species from Chile; *Macrurohelea* Ingram and Macfie, with 12 species, 9 from Argentina and Chile and 3 from Australia; and *Notiohelea* Grogan and Wirth, with one species from Chile.

The purpose of this paper is to describe 4 new species in the tribe Ceratopogonini belonging to 3 rarely collected genera, that were recently taken by GRS in the temperate subantarctic region of southwestern Argentina. The types of these new species are deposited in the collection of the Museo de La Plata, La Plata, Argentina (MLP); paratypes of *Macrurohelea fuscipennis* and *Notiohelea pilosa* will be deposited in the National Museum of Natural History, Washington, D.C. (USNM). In addition, a key to the Neotropical species of *Macrurohelea* is provided which includes the female of *M. paracaudata* Grogan and Wirth (1980) that was recently described by Spinelli (1987).

For an explanation of general ceratopogonid terminology, see Downes and Wirth (1981); for special terms dealing with genera in the tribe Ceratopogonini, see Wirth and Grogan (1988), Grogan and Wirth (1979), and Spinelli and Grogan (1984).

Diaphanobezzia patagonica Spinelli and Grogan, NEW SPECIES

Fig. 1

Diagnosis.—Distinguished from females of *Diaphanobezzia spinellii* Wirth and Grogan (1988) by its sparsely pubescent eyes, longer 4th palpal segment, and wing with longer costa and R4+5.

Holotype female.—*Head:* Dark brown. Eyes broadly separated above, sparsely pu-

bescent between the lower ommatidia. Antennal scape pale brown, bearing 3 pairs of setae; pedicel dark brown; flagellum (Fig. 1a) dark brown, lengths of flagellomeres in proportion of 11-7-7-7-7-6-6-7-8-8-9-10-14; antennal ratio 0.84; flagellomeres 1–8 bearing a pair of trichoid sensilla. Palpus (Fig. 1b) uniformly dark brown; segment lengths in proportion of 3-10-14-15; palpal ratio 3.5. Mandible with 8 coarse teeth.

Thorax: Dark brown. Scutum covered with strong setae, anterior spine absent, 8 prealar setae and 1 postalar seta; scutellum apparently with 6 similar sized bristles. Legs dark brown; tarsomeres 1–4 of mid and hind legs slightly paler brown; femora and mid and hind tibiae armed apically with 1–2 long spines, hind tibia with 7–9 spines on extensor side; hind tibial comb with 6 spines; apices of tarsomeres 1–3 and base of hind tarsomere 1 with a pair of ventral spines, ventral surface of mid tarsomere 1 with 3 pairs of widely spaced spines; hind tarsal ratio 2.3; claws small, evenly curved, equal sized with basal inner teeth. Wing (Fig. 1c) whitish hyaline; anterior veins brownish, distal ½ of costa and R4+5 dark brown, all other veins barely perceptible; r-m crossvein interrupted at middle; cell R5 without intercalary veins; costal finge dense; costal sections 1-II-III in proportion of 28-25-9, R4+5 40; costal ratio 0.92; wing length 1.06 mm, breadth 0.40 mm. Halter (Fig. 1d) pale in color, sac-shaped, lacking a distinct constriction below knob, as is typical of the genus.

Abdomen: Dark brown. Sternites 3–5 entire, with a broad rounded caudal notch; sternite 8 (Fig. 1e) deeply notched caudally with broadly rounded posterior lobes; each arm of sternite 9 (Fig. 1e) slightly hooked; sternite 10 (Fig. 1e) with 2 pairs of setae, the posterior pair longer, cerci short. Spermathecae (Fig. 1e) subequal, slightly ovoid with short necks, each about 0.053 mm in diameter; a small vestigial 3rd spermatheca present.

Type material.—Holotype female labeled "Argentina, Santa Cruz, Rio Pinturas, 15-I-1988, G. R. Spinelli, entomological net," (MLP).

Distribution.—Argentina.

Etymology.—The specific epithet, *patagonica*, refers to the southernmost region of Argentina where the type was collected.

Remarks.—Females of *Diaphanobezzia spinellii* Wirth and Grogan (1988) differ from those of *D. patagonica* n. sp. by their densely pubescent eyes, shorter 4th palpal segment that is less than ½ the length of the 3rd palpal segment, its wing with shorter costa (costal ratio 0.82) and R4+5, complete r-m crossvein, and different costal proportions.

Diaphanobezzia pellucida Ingram and Macfie (1931) is known only from a single male but it differs from *D. patagonica* n. sp. by its larger size (wing length 1.7 mm), having intercalary veins in cell R5, and its r-m crossvein is complete.

This new species, known only from the single female holotype, was collected in the Valley of the Rio Pinturas located in the Patagonian steppe (47°S), approximately 150 km E of the subantarctic forest.

Macrurohelea fuscipennis Spinelli and Grogan, New Species

Fig. 2

Diagnosis.—Distinguished from females of other species in the genus by its bare eyes, wing darkly infuscated on distal ⅔, proximal ⅓ hyaline, and spermathecae with long slender necks.

Female.—*Head:* Yellowish brown. Eyes bare, nearly contiguous. Antennal scape yellow, bearing 2 pairs of setae; pedicel dark brown; flagellum (Fig. 2a) brownish; lengths of flagellomeres in proportion of 30-18-17-17-18-18-19-20-20-20-22-25-32; antennal ratio 0.78 (0.75–0.81, n = 3); flagellomere 1 with 4 sensilla coeloconica, flagellomeres 1–8 with a pair of trichoid sensilla. Palpus (Fig. 2b) yellowish; lengths of segments in

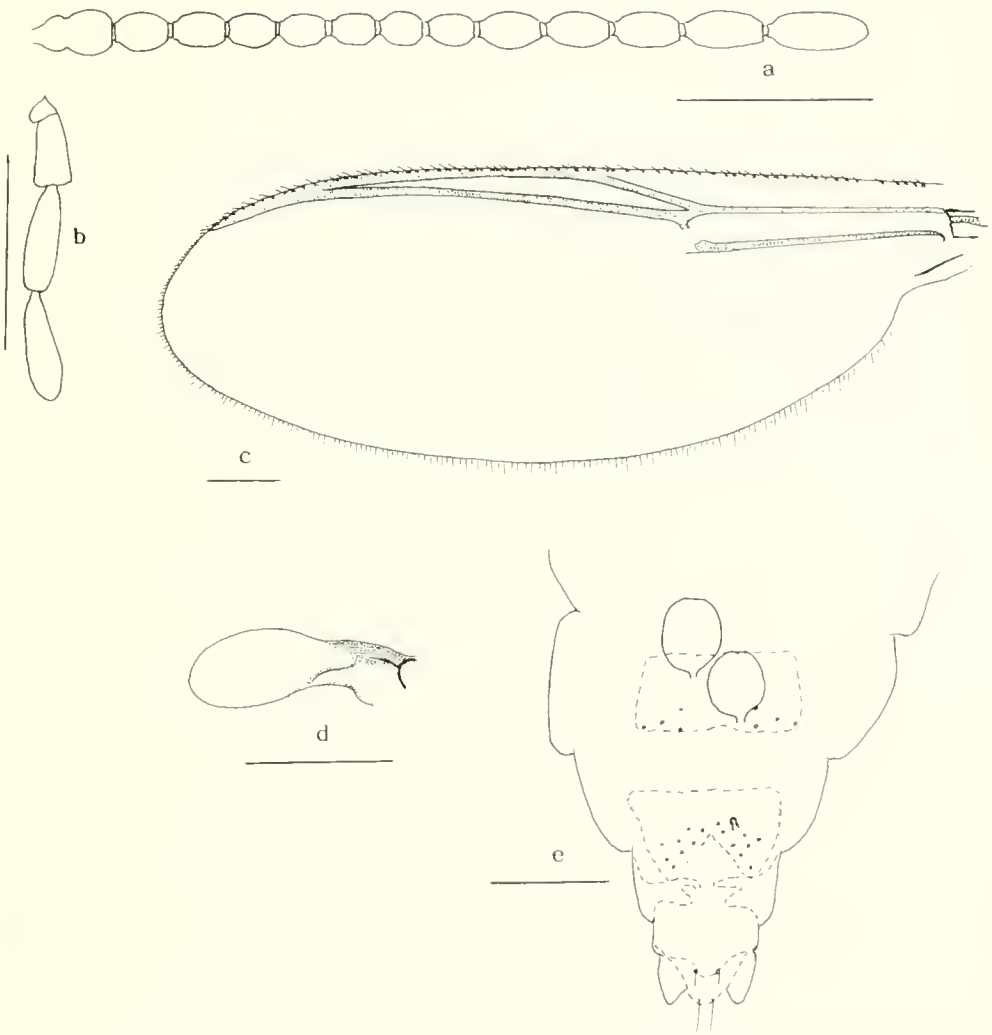

Fig. 1. *Diaphanobezzia patagonica*. a, flagellum; b, palpus; c, wing; d, halter; e, distal portion of abodomen. Scale bars = 0.1 mm.

proportion of 10-15-16-10-18; segment 3 with small sensory pit; palpal ratio 1.70 (1.40–2.00, n = 4). Mandible (Fig. 2c) infuscated at apex, with 8 teeth.

Thorax: Yellowish, humeral pits infuscated, prealar areas dark brown. Scutum (Fig. 2d) covered with fine pubescence, 4 prealar setae, 1 postalar seta; scutellum (Fig. 2d) with 3–5 bristles; postscutellum dark brown. Legs yellowish, tarsomeres 4–5 slightly infuscated; hind tibial comb with 6 spines; hind tarsal ratio 2.1 (n = 4); palisade setae on tarsomere 1 of fore and hind legs; tarsomere 4 cordiform; tarsomere 5 of fore leg 4× longer than broad, 3× longer than broad on mid and hind legs; claws small, equal sized without basal inner teeth. Wing (Fig. 2e) with proximal ⅓ whitish hyaline, veins yellowish, distal ⅔ with membrane and veins darkly infuscated; 2 radial

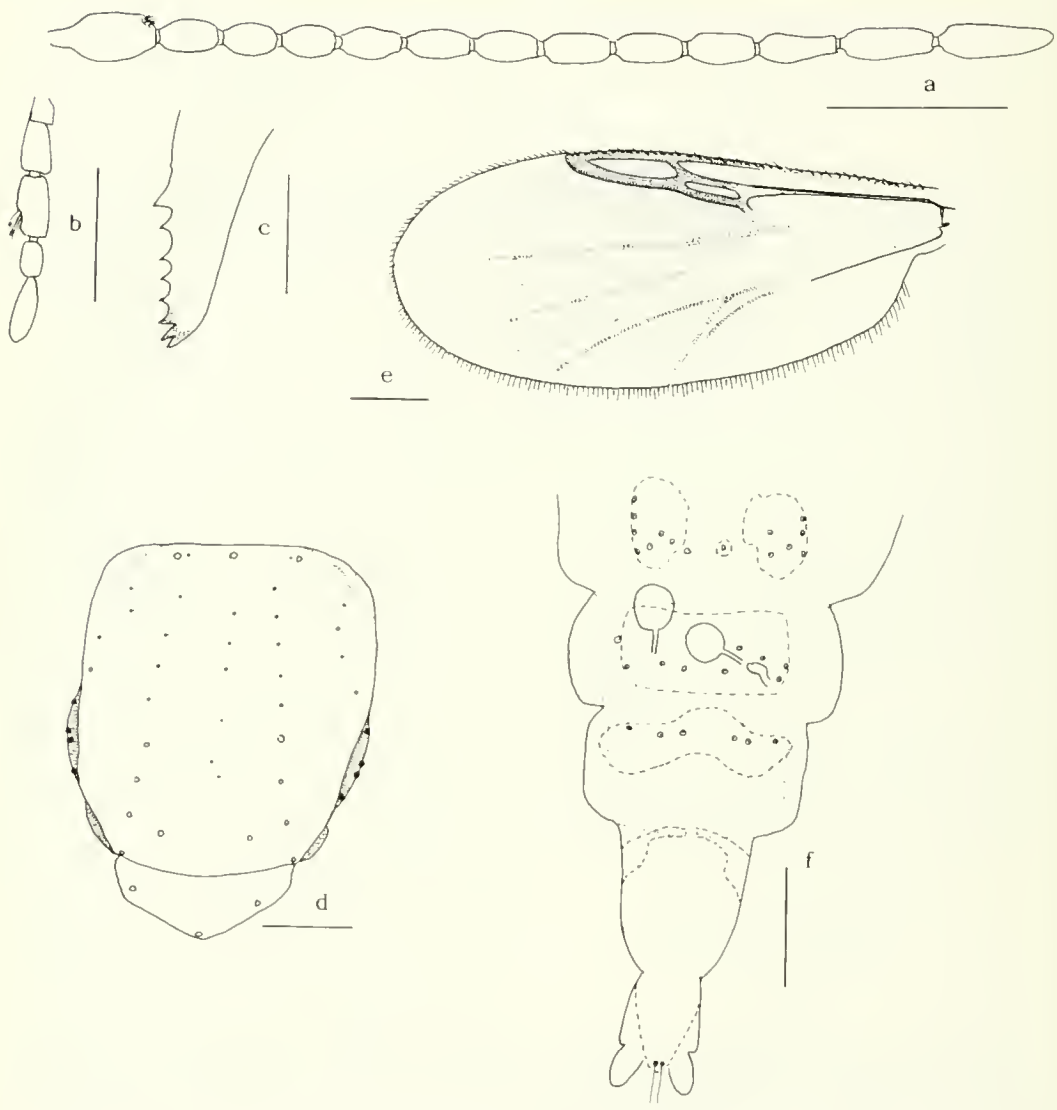

Fig. 2. *Macrurohelea fuscipennis*. a, flagellum; b, palpus; c, mandible; d, scutum and scutellum; e, wing; f, distal portion of abodomen. Scale bars = 0.1 mm (a, d–f), 0.75 mm (b), 0.02 mm (c).

cells, 2nd 1.5× longer than 1st; cell R5 without intercalary veins; costal ratio 0.69 (0.68–0.70, n = 4); wing length 1.18 (1.10–1.26, n = 4) mm, breadth 0.47 (0.45–0.54, n = 4) mm. Halter whitish.

Abdomen: Brown. Sternites 2–6 (Fig. 2f) divided by broad unsclerotized area; sternites 7–8 (Fig. 2f) entire; each arm of sternite 9 (Fig. 2f) slender with truncate tip; sternite 10 (Fig. 2f) with a pair of apical setae, cerci short; segments 9 and 10 elongated and bent forward ventrally as is typical for the genus. Spermathecae (Fig. 2f) subequal, spheroid, with long slender necks, each 0.034 mm in diameter and the neck 0.019 mm long; a small 3rd vestigial spermatheca present.

Type material.—Holotype female, 3 fe-

male paratypes labeled "Argentina, Chubut, Parque Nacional Los Alerces, 'El Alerzal,' 22-I-1988, G. R. Spinelli, entomological net," (MLP).

Distribution.—Argentina.

Etymology.—The specific epithet, *fusci-pennis,* refers to the distinctive wing of this species that is infuscated on its distal portion.

Remarks.—The wing that is darkly infuscated on its distal ⅔ and hyaline on its proximal ⅓ readily distinguishes this species from all other species of *Macrurohelea.* In addition, all other species of *Macrurohelea* (13 species presently known) have pubescent eyes and further differ from *M. fusci-pennis* n. sp. in having spermathecae with shorter necks. *Macrurohelea dycei* Grogan and Wirth (1985) from Australia is the only other species that has spermathecal necks nearly as long, but its spermathecae are ovoid with moderately tapering necks. See the key to the Neotropical species of *Macrurohelea* below for further ways that this new species differs from others in the genus.

This new species is presently known from only 4 females which were collected in the temperate subantarctic forest of Argentina.

Macrurohelea similis Spinelli and Grogan, New Species

Fig. 3a, b

Diagnosis.—Distinguished from males of other species of *Macrurohelea* by the following combination of characters: small size (wing length 0.95 mm), wing without intercalary veins in cell R5, gonostylus extending ⅓ of its length beyond tergite 9.

Holotype male.—*Head:* Dark brown. Eyes pubescent, nearly contiguous. Antenna with pale scape; pedicel dark brown; flagellum and plume brown, flagellomeres distinctly separated with lengths in proportion of 20-8-7-7-7-6-6-6-7-12-15-9; flagellomere 1 with 2 sensilla coeloconica; antennal ratio 0.44. Palpus brown; segment lengths in proportion of 5-8-9-6-11; segment 3 with well defined sensory pit.

Thorax: Dark brown. Scutum with 4 prealar setae and 1 postalar seta; scutellum with 3 large and 2 small bristles. Legs uniformly brown; hind tibial comb with 6 spines; hind tarsal ratio 2.2; palisade setae on fore and mid tarsomere 1; claws small, equal sized with bifid tips. Wing with membrane slightly infuscated, veins brown; 1st radial cell subequal to 2nd; cell R5 without intercalary veins; costal ratio 0.66; wing length 0.95 mm, breadth 0.36 mm. Halter stem brown; knob white.

Abdomen: Brown. Genitalia as in Fig. 3a, b. Sternite 9 moderately long, twice as broad as long, tapered basally, posterior margin straight; tergite 9 moderately short, triangular, gradually tapering distally with a quadrate posterolateral extension and slender pubescent cerci which are divergent and extend beyond tip of quadrate extensions. Gonocoxite slightly curved, 2.5× longer than broad with a small mesobasal lobe; gonostylus shorter than gonocoxite, greatly curved, gradually tapering to a slender pointed tip. Aedeagus short, triangular, slightly broader than long, basal arch about ½ of total length; basal arm nearly straight, heavily sclerotized; distal portion tapering to a moderately pointed tip. Parameres (Fig. 3b) heavily sclerotized, separate; basal arm short, broad basally, pointed apically; distal portions slender, closely approximated proximally, divergent distally, tapering near apex to a slightly bent pointed tip.

Type material.—Holotype male labeled "Argentina, Rio Negro, Parque Nacional Nahuel Huapi, camino a cascada de los Alerces, 24-I-1988, G. R. Spinelli, entomological net," (MLP).

Distribution.—Argentina.

Etymology.—The specific epithet, *similis,* is a reference to the similarity of the genitalia of this new species to those of *Macrurohelea caudata* Ingram and Macfie (1931).

Remarks.—*Macrurohelea similis* n. sp. most closely resembles *M. caudata* Ingram

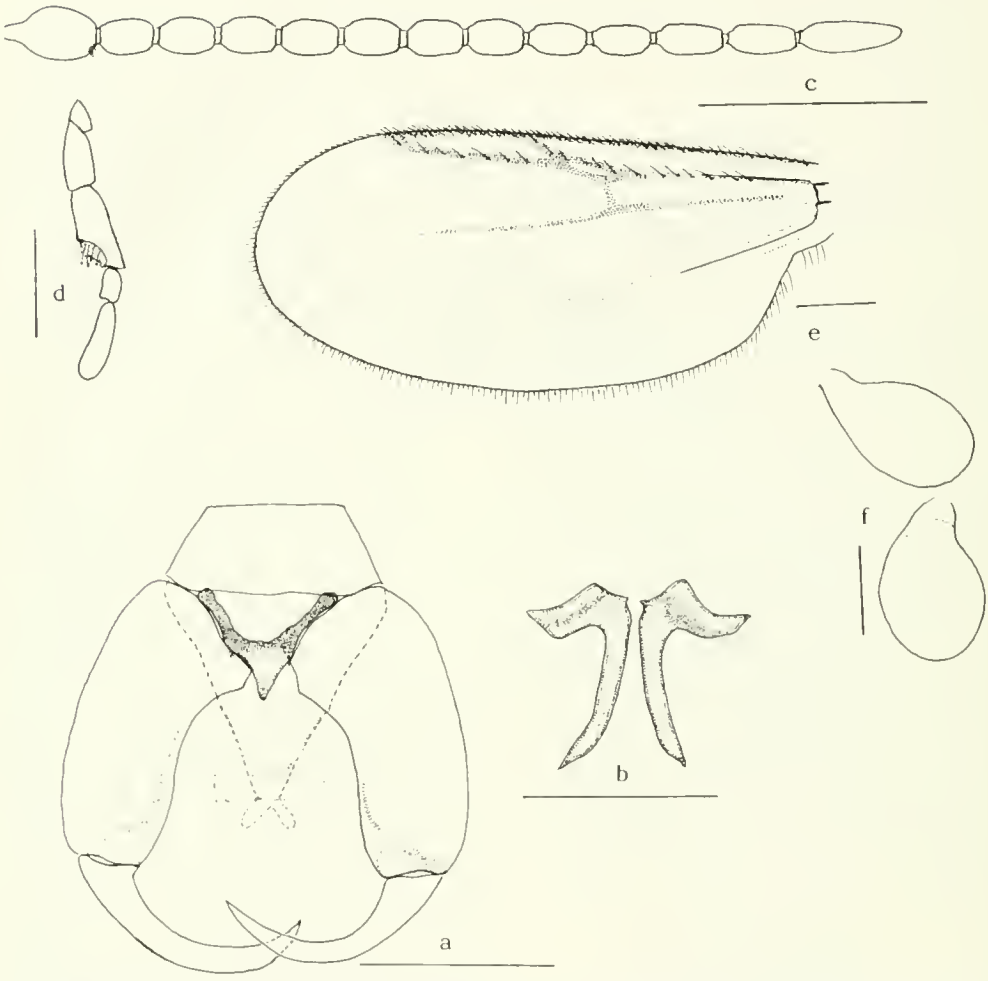

Fig. 3. *Macrurohelea similis*, a, b, and *Notiohelea pilosa*, c–f. a, genitalia (parameres removed); b, parameres; c, flagellum; d, palpus; e, wing; f, spermathecae. Scale bars = 0.1 mm (a–c, e), 0.05 mm (d), 0.025 mm (f).

and Macfie (1931) by virtue of their similar male genitalia. However, *M. caudata* differs from this new species by several features of its genitalia such as, aedeagus broader distally with a square tip, cerci that arise from ventral surface of tergite 9 but do not extend beyond tergite 9, gonocoxite that is straight, and parameres with different shaped basal arm and distal portions parallel. In addition, *M. caudata* has eyes that are widely separated and bare except on extreme inner margins, and the 3rd palpal segment is longer than 5th (5th segment longer than 3rd in *M. similis* n. sp.). See the key to the Neotropical species of *Macrurohelea* below for further ways in which this new species differs from other species in the genus.

This new species, which is presently known only from the male holotype, was collected in the temperate subantartic forest of Argentina.

Key to the Neotropical Species of *Macrurohelea*

1. Females 2
– Males 11
2. One spermatheca 3
– Two spermathecae 4

3. Wing with intercalary veins in cell R5; wing membrane infuscated, veins dark brown ..... *monotheca* Spinelli and Grogan
– Wing without intercalary veins in cell R5; wing membrane whitish hyaline, veins pale ..... *gentilii* Spinelli and Grogan
4. Wing with intercalary veins in cell R5 5
– Wing without intercalary veins in cell R5 .. 6
5. Second radial cell of wing 2.5× longer than 1st, veins brown; antennal ratio 1.61 ..... *wirthi* Spinelli and Grogan
– Second radial cell of wing 3× longer than 1st, veins pale; antennal ratio 1.00 ..... *caudata* Ingram and Macfie
6. Second radial cell of wing twice as long as 1st 7
– Second radial cell of wing at least 3× longer than 1st 10
7. Flagellum very short, flagellomeres 9–12 broader than long, antennal ratio 0.59; very small species, wing length 0.94 mm ..... *kuscheli* Wirth
– Flagellum longer, flagellomeres 9–12 twice as long as broad, antennal ratio 0.75–1.16; small species, wing length 1.02–1.42 mm 8
8. Wing membrane hyaline, veins gray ..... *irwini* Grogan and Wirth
– Wing membrane infuscated on at least distal ⅔, veins brown 9
9. Wing membrane infuscated on distal ⅔, proximal ⅓ hyaline; tips of claws pointed; spermathecae with very long necks ..... *fuscipennis*, new species
– Wing membrane entirely infuscated; tips of claws bifid; spermathecae with shorter necks ..... *paracaudata* Grogan and Wirth
10. Flagellomeres 5–8 with apical sensilla coeloconica; legs with inconspicuous setae; wing membrane and veins pale ..... *thoracica* Ingram and Macfie
– Flagellomeres 5–8 without apical sensilla coeloconica; legs with numerous long bristly setae; wing membrane and veins infuscated dark brown ..... *setosa* Wirth
11. Large species, wing length 2.1 mm or greater 12
– Smaller species, wing length 1.5 mm or less 13
12. Legs with long bristly setae; wing membrane and veins infuscated dark brown *setosa* Wirth
– Legs with inconspicous setae; wing membrane and veins pale ..... *thoracica* Ingram and Macfie
13. Very small species, wing length 0.90–0.95 mm 14
– Small species, wing length 1.3 mm or greater 15
14. Sternite 9 with caudomedial notch; gonostylus extends to apex of tergite 9 ..... *paracaudata* Grogan and Wirth
– Sternite 9 without caudomedial notch; gonostylus extends ⅓ of its total length beyond apex of tergite 9 ..... *simulis*, new species
15. Wing with intercalary veins in cell R5, 2nd radial cell subequal to 1st; aedeagus more or less crescent shaped ..... *caudata* Ingram and Macfie
– Wing without intercalary veins in cell R5, 2nd radial cell 1.7–2.0× longer than 1st; aedeagus triangular 16
16. Gonostylus bent abruptly subapically at 90°; sternite 9 with deep caudomedial excavation ..... *gentilii* Spinelli and Grogan
– Gonostylus curved subapically, not bent at 90°; sternite 9 with shallow caudomedial excavation ..... *irwini* Grogan and Wirth

Notiohelea pilosa Spinelli and Grogan, New Species
Fig. 3c–f

Diagnosis.—Distinguished from its only known congener, *N. chilensis* Grogan and Wirth (1979), by its pubescent eyes, more darkly infuscated wing with the 2nd radial cell over 3× longer than 1st, shorter proboscis, more slender 3rd palpal segment, and ovoid spermathecae.

Female.—*Head:* Brown. Eyes pubescent, narrowly separated. Antennal scape pale, bearing 3 pairs of setae; pedicel dark brown; flagellum (Fig. 3c) brown, lengths of flagellomeres in proportion of 22-13-14-14-14-13-13-13-13-14-15-16-20; antennal ratio 0.71 (0.67–0.74, n = 3); flagellomere 1 with 5 sensilla coeloconica, flagellomeres 1–8 bearing a pair of trichoid sensilla. Palpus (Fig. 3d) brown; segment lengths in proportion of 9-16-20-8-14; palpal ratio 2.10 (2.05–2.25, n = 3); segment 3 with a moderately broad apical sensory pit bearing 4–5 capitate sensilla. Proboscis short, proboscis/head ratio 0.42 (0.40–0.44, n = 2). Mandible reduced, vestigial, without teeth.

Thorax: Brown. Scutum densely covered with coarse setae, humeral pits present, no anterior spine, 3 prealar setae and 1 postalar seta; scutellum with 4 similar sized bristles and 6 smaller setae. Legs brown, nearly identical with those of *N. chilensis* in form and features; hind tarsal ratio 1.75 (n = 3). Wing (Fig. 3e) membrane darkly infuscated (infuscation not depicted in Fig. 3e), covered with coarse microtrichia; veins brown,

veins R1 and R4+5 with macrotrichia; 2 radial cells present, the 2nd 3.2× longer than 1st. Halter brown.

Abdomen: Brown. Moderately broad proximally, tapering distally at segment 5; sternite 10 with one pair of large setae; 2 ovoid, subequal spermathecae (Fig. 3f), each 0.045 mm long with neck and 0.03 mm wide.

Type material.—Holotype female labeled "Argentina, Chubut, Parque Nacional Los Alerces, 'El Alerzal,' 22-I-1988, G. R. Spinelli, entomological net," (MLP); 2 female paratypes, 1 with same data as holotype, 1 with same data as holotype except taken 23-I-1988 by CDC light trap.

Distribution.—Argentina.

Etymology.—The specific epithet, *pilosa,* is a reference to the coarse setae that cover the scutum of this species.

Remarks.—The only other known species in the genus, *Notiohelea chilensis* Grogan and Wirth (1979), differs from *N. pilosa* n. sp. by its bare eyes, longer proboscis (proboscis/head ratio 0.56), broader 3rd palpal segment (palpal ratio 1.82), spherical spermathecae, and more lightly infuscated wing with the 2nd radial cell only twice as long as the 1st.

This species is currently known only from female specimens that were collected in the temperate subantarctic forest of Argentina.

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IDENTITY OF *ENCARSIA* SPP. (HYMENOPTERA: APHELINIDAE) INTRODUCED INTO WESTERN SAMOA FOR BIOLOGICAL CONTROL OF *PSEUDAULACASPIS PENTAGONA* (TARGIONI-TOZZETTI) (HEMIPTERA: DIASPIDIDAE)

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Abstract.—Cultures of *Encarsia* spp. thought to be *E. berlesei* (Howard) from the USA, France and Tonga, were imported into Western Samoa for biological control of *Pseudaulacaspis pentagona* (Targioni-Tozzetti), a pest on passion fruit vines (*Passiflora edulis* var. *flavicarpa* Degener). Comparison of specimens from the cultures with the syntypes of *E. berlesei* and *E. diaspidicola* (Silvestri) revealed both species were present. Both species were released but only *E. diaspidicola* proved to be an effective biological control agent.

Key Words: *Encarsia, diaspidicola, berlesei, Pseudaulacaspis, Passiflora,* biological control, Western Samoa

White peach scale, *Pseudaulacaspis pentagona* (Targioni-Tozzetti) is a serious pest on several unrelated plants in many countries (Clausen et al. 1978). In Western Samoa *P. pentagona* is a recently-introduced pest of passionfruit (*Passiflora edulis* var. *flavicarpa* (Degener), where it has contributed to a reduction of 43% in the value of pulp produced between 1984 and 1986 (Peters et al. 1985, Rasch 1986).

The aphelinid parasitoid *Encarsia berlesei* (Howard) has been recorded as an effective biological control agent for *P. pentagona* in several countries (Clausen et al. 1978). Unlike *E. berlesei,* the closely-related *E. diaspidicola* (Silvestri) has not been recognized as an effective biological control agent (Greathead 1971, Waterhouse and Norris 1987). Moreover, *E. diaspidicola* has been considered a synonym of *E. berlesei* by Flanders (1960) and Greathead (1976) despite characteristics noted by Silvestri (1930) that enabled its separation from *E. berlesei.*

In 1986, three cultures of *Encarsia* spp., all presumed to be *E. berlesei,* were imported into Western Samoa from the USA, France and Tonga for biological control of *P. pentagona.* One species, subsequently identified as *E. diaspidicola,* became an effective biological control agent for this scale insect (Liebregts et al. 1989). Observed differences between specimens from the USA and those from the other two localities, and difficulties with their identification, prompted a comparison of specimens from all cultures imported in Western Samoa with type specimens of *E. berlesei* and *E. diaspidicola.*

Materials and Methods

The following were examined:

E. berlesei: Six syntypes on slide bearing two labels (white)—"9942, *Prospaltella ber-*

Table 1. Comparative forewing measurements of *Encarsia* spp.

	No. of Specimens Examined	Measurement[a]		Measurement[b]	
		$\bar{x}$	Range	$\bar{x}$	Range
E. berlesei					
Washington, D.C., USA (syntypes)	5	0.12	0.11–0.12	0.37	0.35–0.37
Gainsville, Florida, USA	6	0.10	0.09–0.12	0.37	0.36–0.37
Upolu, W. Samoa (field recoveries)	3	0.12	0.11–0.12	0.36	0.36–0.37
E. diaspidicola					
Capetown, South Africa (syntypes)	4	0.21	0.20–0.22	0.31	0.30–0.31
France (CIBC culture)	7	0.21	0.20–0.22	0.32	0.30–0.32
Tongatapu, Tonga	5	0.21	0.20–0.22	0.32	0.31–0.32
Upolu, W. Samoa (field recoveries)	7	0.22	0.21–0.23	0.32	0.31–0.32

[a] Maximum fringe length/wing length.
[b] Maximum wing width/wing length.

lesei How. on lilac, Washington, D.C., E. R. Sassocei, 2 June 1906"; (red) "Type No. 9942 U.S.N.M." in U.S. National Museum, Washington, D.C., USA.

E. diaspidicola: Nine syntypes on slide bearing two labels (white)—"*Prospaltella diaspidicola* Silv. (Cotypes) *Encarsia diaspidicola* (Silv.) Capetown, S. Afr."; (red) "Cotype No. 41387 U.S.N.M" in U.S. National Museum, Washington, D.C., USA and four specimens on slide bearing one label "*Prospaltella diaspidicola* 10, 1[a] generaz. italia Portici—vii. 1909" in the University of Naples, Italy.

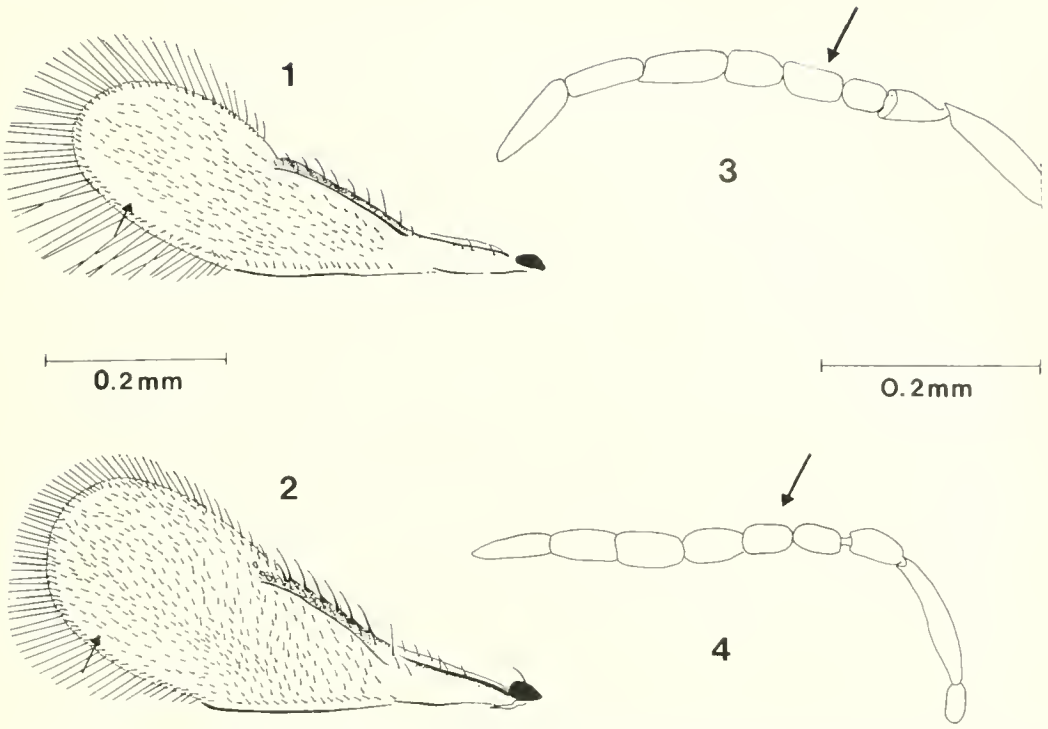
Specimens of *Encarsia* spp., cultures from Gainsville, Florida, USA (R. I. Sailer), France (CIBC), Tonga (field collected) and Western Samoa (field collected after establishment) were slide mounted for comparison with the syntypes of *E. berlesei* and *E. diaspidicola*. All cultures were uniparental.

Results and Discussion

We have compared the syntypes of *E. berlesei* and *E. diaspidicola* with specimens from the three cultures introduced into Western Samoa (Table 1). Despite slight differences observed (in forewing fringe length) between material from Gainsville, Florida, USA and the syntypes of *E. berlesei* from Washington, D.C., USA, we conclude that the two are conspecific. We also conclude that materials obtained from France and from Tonga are conspecific with the syntypes of *E. diaspidicola* from South Africa.

We have had no difficulty in distinguishing the two *Encarsia* spp., based on Silvestri's (1909) original description of *E. diaspidicola*, his (1930) subsequent comparison of the two species and the differences noted by Gahan (1925). In addition to forewing measurements (Table 1), we have found the following characteristics most useful for distinguishing the two species: the outer forewing margin of *E. diaspidicola* (Fig. 1) is more narrowly rounded than *E. berlesei* (Fig. 2) and there is an area almost free of setae close to the outer margin in *E. diaspidicola*, whereas on the forewing of *E. berlesei* the discal setae extend uninterrupted to the marginal fringe. Funicle segment 2 of the antenna of *E. diaspidicola* (Fig. 3) is clearly longer than segment 1 whereas in *E. berlesei* (Fig. 4) segments 1 and 2 are subequal.

We consider that the identification of these two parasitoids of *P. pentagona* may have been confused in biological control programs. Flanders (1960) considered *E. diaspidicola* to be a synonym of *E. berlesei* without explanation and Greathead (1971) stated that the former was unable to control *P. pentagona* in Europe. In view of the success of Tongan and French *E. diaspidicola* in controlling *P. pentagona* in Western Samoa,



Figs. 1–4. *Encarsia* spp. 1, 2, Forewings of syntypes: *E. diaspidicola* (Silvestri) and *E. berlesei* (Howard), respectively. 3, Antenna of *E. diaspidicola* (Tonga). 4, Antenna of *E. berlesei* (Florida, USA). Arrows indicate areas clear of setae (1, 2) and second funicle segment (3, 4).

some examples attributed to *E. berlesei* may actually refer to *E. diaspidicola*. A taxonomic re-assessment of the *Encarsia* spp. from biological control programs is clearly warranted.

In Western Samoa, *E. diaspidicola* has maintained biological control of *P. pentagona* since its establishment in 1986 (Liebregts et al. 1989). Apart from early field recoveries over a five month period following its release, we have no further evidence for establishment of *E. berlesei*.

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Note

Baetis jesmondensis McDunnough, a New Junior Synonym of *Baetis tricaudatus* Dodds (Ephemeroptera: Baetidae)

In their revision of the Nearctic *Baetis* species, Morihara and McCafferty (1979. Trans. Am. Entomol. Soc. 105: 139–221) inadvertently omitted *Baetis jesmondensis* McDunnough from their account of species synonymies. They had found the species equivalent to *Baetis tricaudatus* based on an examination of the type material and larvae tentatively assigned to *B. jesmondensis*. Our recent rediscovery and review of this material leads to the same conclusion, fully substantiating the previous conclusion of Morihara and McCafferty.

Members of the Holarctic *Baetis rhodani* species group, to which *B. tricaudatus* and *B. jesmondensis* belong, demonstrate considerable morphological variation with respect to developmental temperature gradients and geographic distribution. The adult types of *B. jesmondensis* are clearly within the known range of variation of *B. tricaudatus*. Furthermore, our examination of numerous larval series from the northwestern United States and southwestern Canada, including those assumed to be *B. jesmondensis* and taken from its type locality, showed that all larvae fell within the concept of *B. tricaudatus*. All of these data lead us to reaffirm that the two names are synonymous. We therefore designate *B. jesmondensis* McDunnough as a junior synonym of *Baetis tricaudatus* Dodds, New Synonym.

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FIRST DISTRIBUTIONAL RECORDS OF TABANIDAE (DIPTERA) IN CONNECTICUT

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Abstract.—First distributional records from Connecticut are given for *Atylotus sphagnicola* Teskey, *Chrysops celatus* Pechuman, *C. hinei* Daecke, *C. nigribimbo* Whitney, *Goniops chrysocoma* (Osten Sacken), *Hybomitra daeckei* (Hine), *H. frosti* Pechuman, *H. longiglossa* (Philip), *H. lurida* (Fallen), *H. minuscula* (Hine), *H. nitidifrons nuda* (McDunnough), *H. trepida* McDunnough, *H. zonalis* (Kirby), *Stonemyia isabellina* (Wiedemann), *Tabanus fulvicallus* Philip, and *T. vivax* Osten Sacken. Habitats and flight periods of most species are discussed.

Key Words: bog, fen, *Atylotus, Chrysops, Goniops, Hybomitra, Stonemyia, Tabanus*

Fairchild (1950) summarized distributional records of deer flies and horse flies in Connecticut. His synopsis, however, is outdated as a result of nomenclatural changes, descriptions of new species, and new state collection records. A current assessment of tabanids in Connecticut would be valuable in light of their considerable importance as nuisance pests and carriers of infectious agents (Krinsky 1976). During the last decade, I have collected tabanids throughout Connecticut to provide new data for my planned revision of Fairchild's (1950) monograph. My extensive sampling of bogs and fens and examination of museum specimens have resulted in many new tabanid records. Here I report the first distributional data for 16 tabanid species in Connecticut to make the information available for the database of North American Diptera which is now in preparation.

MATERIALS AND METHODS

Sampling sites in Connecticut are identified by county, town (geographical subdivision of a county), and additional information if available. The number and sex of tabanids collected on a given date or by a certain method are given in parentheses. Adults were captured with a hand-held insect net or with a Malaise or canopy trap. The use of the horizontal Malaise trap (D. Focks and Co., P.O. Box 12852, Gainesville, Florida 32608) is discussed by Maier (1984). The canopy trap, which is pictured by Pechuman (1981, Fig. 9), was baited with ca. 4 kg of dry ice to increase the number of specimens captured.

Voucher specimens of tabanids except *Stonemyia isabellina* (Wiedemann) are deposited in the insect collection at The Connecticut Agricultural Experiment Station, New Haven. The adult specimen of *S. isabellina* is retained in the author's collection.

COLLECTION RECORDS AND COMMENTS

Atylotus sphagnicola Teskey

Collection records.—Hartford Co., Burlington, bog near Covey Road, 27 May 1986 (1 ♂). Litchfield Co., Salisbury, shrubby bog by Bingham Pond, 14–16 June 1983, horizontal Malaise trap (1 ♂), 21 June 1985,

horizontal Malaise trap (1 ♀), 12 July 1984, horizontal Malaise trap (1 ♀).

Based on collection records given by Teskey (1983) and those presented here, this species apparently is restricted to sphagnum bogs. In Connecticut, adults fly in parts of bogs dominated by ericaceous shrubs. *Atylotus sphagnicola* was recorded previously from northwestern Connecticut (Teskey 1983), but the record is erroneous (Teskey, personal communication 1985). My collection localities are the two southernmost to date. In Connecticut, adults have been collected between 27 May and 12 July.

Chrysops celatus Pechuman

Collection records.—Litchfield Co., Cornwall, Mohawk Pond, 19 July 1979 (1 ♀), near Hollenbeck River at junct. Conn. Highways 43 and 63, 4 August 1987 (1 ♀); Kent, Leonard Pond Swamp, 9 July 1979 (1 ♀), Mud Pond, 20 July 1979 (4 ♀); Norfolk, marsh at edge of Beckley Pond, 7 July 1986, horizontal Malaise trap (2 ♀). Middlesex Co., East Haddam, bog at north end of Lake Hayward, 3 July 1984, canopy trap (8 ♀), 17 July 1977 (1 ♀), 1–2 August 1984, canopy trap (2 ♀). New Haven Co., Branford, 30 July 1985 (2 ♀), near Stony Creek, 28 July 1948 (1 ♀); Guilford, 4.5 km NNW junct. Conn. Highways 77 and 80, 27 July 1985 (1 ♀); Hamden, 12 July 1928 (1 ♀); New Haven, 9 June 1911 (1 ♀), 28 June 1911 (1 ♀); Madison, 14–15 June 1979, Malaise trap baited with dry ice (1 ♀); Meriden, South Meriden, 7 July 1935 (1 ♀). New London Co., Voluntown, fen in Atlantic white cedar swamp by Beachdale Pond, 19 June 1985, horizontal Malaise trap baited with dry ice (2 ♀), 10 July 1984, horizontal Malaise trap (5 ♀), 16 July 1986, canopy trap (2 ♀), 16–17 July 1986, horizontal Malaise trap baited with dry ice (6 ♀), 7 August 1984, hovering over human (5 ♀), horizontal Malaise trap baited with dry ice (2 ♀), 17 August 1984, hovering over human (1 ♀), Pachaug St. Forest, near Hodge Pond, 21 June 1986 (4 ♀). Tolland Co., Hebron, Tom 2-Pony, Kinney Road, 7 July 1979 (2 ♀); Mansfield, Mt. Hope River, Laurel Lane, 24 June 1979 (1 ♀); Somers, 12 July 1979 (1 ♀); Tolland, near Tolland Marsh Pond, 28 June 1988, canopy trap (5 ♀); Union, Bigelow Hollow St. Park, 16 July 1979 (2 ♀); Willington, 1.5 km NNE West Willington, black spruce bog, 30 June 1982 (1 ♀). Windham Co., Ashford, Elliot Road, 24 June 1979 (1 ♀); 28 June 1979 (5 ♀), Great Oak Road, 6 July 1979 (1 ♀); Plainfield, cedar swamp, 13 July 1979 (1 ♀); Putnam, 8 July 1953 (4 ♀); Woodstock, Old Turnpike Road, 16 July 1979 (1 ♀).

Pechuman (1949) originally described *C. celatus* as a subspecies of *C. flavidus* Wiedemann. Fairchild (1950) recorded *C. flavidus* from Connecticut, but specimens examined by him are a mixture of *C. celatus* and *C. flavidus*. *Chrysops celatus* is a common species that occurs in a variety of habitats throughout Connecticut. Adults have been captured between 9 June and 17 August.

Chrysops hinei Daecke

Collection records.—Middlesex Co., Deep River, Cockaponset St. Forest, 12–13 August 1977, horizontal Malaise trap (3 ♀); East Haddam, bog at north end of Lake Hayward, 1–2 August 1984, canopy trap (1 ♀); Killingworth, 3 km NW junct. Conn. Highways 81 and 148, 13 August 1985 (3 ♀). New Haven Co., North Haven, 27 August 1983 (1 ♀). New London Co., North Stonington, 3 km WNW Clarks Falls, 14 August 1985 (2 ♀).

This late season deer fly is found mainly in boggy or swampy areas of Connecticut. Jones and Anthony (1964) also reported that it was restricted to swamps. My records indicate adults fly from 1 to 27 August in Connecticut. Lawrence et al. (1976) captured adults in Maryland from 1 August to 12 September.

Chrysops nigribimbo Whitney

Collection records.—Litchfield Co., Cornwall, Mohawk Pond, 19 July 1979 (2 ♀). Middlesex Co., East Haddam, bog at north end of Lake Hayward, 17 July 1985 (2 ♀), 7 August 1986 (1 ♀). New London Co.,

Voluntown, 2 km NE town center, 7 August 1984 (1 ♀). Windham Co., Ashford, Elliot Road, 24 June 1979 (3 ♀), 28 June 1979 (3 ♀).

This species has been captured between 24 June and 7 August in Connecticut, where it is distributed widely.

Goniops chrysocoma (Osten Sacken)

Collection records.—New Haven Co., Guilford, 4.5 km NNW junct. Conn. Highways 77 and 80, 21 July 1983 (1 ♀), 4.0 km NW junct. Conn. Highways 77 and 80, 21 July 1987 (1 ♀).

Both females were resting on vegetation at the edge of a large coastal red maple swamp. My distribution records are the first from New England.

Hybomitra daeckei (Hine)

Collection records.—New Haven Co., Guilford, Chaffinch Island, 14 June 1986 (3 ♀), 19 June 1985 (12 ♀), 19 June 1986 (12 ♀), 26 June 1986 (2 ♀), 3 July 1985 (9 ♀), 15 July 1989 (7 ♀), all from canopy traps. New London Co., Old Lyme, 1 km S junct. Interstate Highway 95 and Conn. Highway 156, 3 July 1986, canopy trap (2 ♀).

All Connecticut localities with *H. daeckei* are salt-marshes where larvae apparently develop. In Connecticut, adults have been trapped between 14 June and 15 July. This flight period is similar in length to the one of 30 May to 26 June recorded in Maryland (Lawrence et al. 1976).

Hybomitra frosti Pechuman

Collection records.—Litchfield Co., Cornwall, Mohawk St. Forest, black spruce bog, 12 August 1986, canopy trap (2 ♀); Norfolk, bog by Beckley Pond, 22 July 1987 (1 ♀).

This species is restricted to sphagnum bogs and possibly fens (Pechuman 1960, 1981, Baribeau and Maire 1983a, b). I collected my three specimens in bogs where the sphagnum mat was shaded partially by black spruce, *Picea mariana* (Miller) Britton, Sterns, and Poggenburg, and by ericaceous shrubs. Shade may be necessary for larval survival because Baribeau and Maire (1983b) found most of their larvae in a forested portion of an ombrotrophic bog. Based on Connecticut records, adult activity lasts from 21 July to 11 August. This flight period is similar in time and length to that observed in Quebec by Baribeau and Maire (1983c).

Hybomitra longiglossa (Philip)

Collection records.—Litchfield Co., Norfolk, bog by Beckley Pond, 23 May 1988 (1 ♂), 27 May 1988 (1 ♂, 1 ♀), 29 May 1987, canopy trap (13 ♀).

Adults are active at peat pools in the bog mat where ericaceous shrubs are sparse and rarely exceed 0.5 m in height. Males apparently take stations at pool margins because they chase flying insects that pass by them and they mate by pools. This species probably is confined to sphagnum bogs where larvae develop (Teskey and Burger 1976). The specimens captured in Connecticut extend the known range of *H. longiglossa* southward by one state. In Ontario, adults are active from 3 to 29 June (Pechuman et al. 1961).

Hybomitra lurida (Fallen)

Collection records.—Litchfield Co., Canaan, junct. Conn. Highway 126 and Page Road, 23 May 1988 (1 ♀); Norfolk, bog by Beckley Pond, 29 May 1987 (1 ♀); Salisbury, near Bingham Pond, 23 May 1987 (1 ♀).

Adults of this uncommon species are known only from the three localities in northwestern Connecticut listed above. These collection sites are the southernmost ones recorded for this species. Its 2-week flight period in May is about one-half the length of that observed elsewhere in northeastern North America (Lewis and Bennett 1977, Maire 1984a, White et al. 1985).

Hybomitra minuscula (Hine)

Collection records.—Hartford Co., Burlington, 15 July 1976 (5 ♀), 19 July 1976 (3 ♀), bog by Lamson Corner, 25 June 1986,

horizontal Malaise trap baited with dry ice (2 ♀), 9 August 1985 (11 ♀); East Windsor, bog at junct. Morris and Wapping Roads, 22 August 1985 (3 ♂, 3 ♀). Litchfield Co., Norfolk, bog by Beckley Pond, 30 June 1958 (1 ♂), 7 July 1986, canopy trap (3 ♀), horizontal Malaise trap baited with dry ice (2 ♀), 7–8 July 1986, horizontal Malaise trap (2 ♀), 17 July 1958 (2 ♀), 17 July 1970 (1 ♂, 3 ♀), 2 August 1960 (1 ♀), 12 August 1986 (2 ♀), bog by Pond Hill Pond, 12 August 1986 (1 ♀), bog by Tobey Pond, 12 August 1986 (2 ♀), 5 km S town center, 3 August 1984 (1 ♀); Salisbury, bog by Bingham Pond, 12 July 1984, canopy trap (2 ♀), 21–23 July 1983, horizontal Malaise trap (3 ♂, 2 ♀), 3 August 1984, canopy trap (1 ♀). Middlesex Co., East Haddam, bog at north end of Lake Hayward, 3 July 1984 (2 ♀), 24 July 1985 (2 ♂, 1 ♀), 1–2 August 1984, canopy trap (1 ♀), 13 August 1985 (1 ♂, 2 ♀), 21 August 1984, canopy trap (1 ♀); Killingworth, 1.3 km SE Kroopa Pond, 19 July 1973 (1 ♀). New Haven Co., Bethany, 4 August 1951 (2 ♀). New London Co., North Stonington, 3 km WNW Clarks Falls, 14 August 1985 (1 ♂); Voluntown, fen in Atlantic white cedar swamp by Beachdale Pond, 16–17 July 1986, horizontal Malaise trap (1 ♀), 17 August 1984 (1 ♀). Tolland Co., Willington, 1 km SSW junct. Interstate Highway 84 and Conn. Highway 32, black spruce bog, 30 June 1982 (5 ♀), 12 August 1982 (2 ♂, 2 ♀), 0.6 km N junct. Conn. Highways 74 and 320, 13 August 1985 (3 ♂, 3 ♀). Windham Co., Plainfield, 4 km E town center, 10 July 1984 (1 ♀), 20 July 1983 (1 ♂, 2 ♀), 4 August 1982 (1 ♀), 19 August 1983 (1 ♀); Windham, 1.8 km W town center, bog by Plains Road, 13 August 1985 (3 ♀).

In Connecticut, this species occurs exclusively in sphagnum bogs which are the only known larval habitats (Teskey 1969). Baribeau and Maire (1983b) found *H. minuscula* to be the most common tabanid in open areas of bogs. My observations agree fully with their assessment. In open areas of Connecticut bogs, males commonly hover about 1 m above the bog mat while they seek females. My observations indicate adults are active between 25 June and 22 August in Connecticut. The flight period in southwestern Ontario is nearly identical in time and duration (Judd 1958).

Hybomitra nitidifrons nuda (McDunnough)

Collection records.—Hartford Co., Burlington, bog by Lamson Corner, 27 May 1986 (3 ♀). Litchfield Co., Canaan, Robbins Swamp, 23 May 1985 (1 ♀); Cornwall, Mohawk St. Forest, black spruce bog, 11 June 1987 (1 ♀); Norfolk, bog by Beckley Pond, 23–27 May 1988, horizontal Malaise trap (5 ♀), 29 May 1987, canopy trap (4 ♀), 4 km WSW town center, 7 June 1984 (1 ♀), 5 km S town center, 7 June 1984, canopy trap (3 ♀); Salisbury, Benton Hill Fen, 11 June 1987, canopy trap (2 ♀), bog by Bingham Pond, 23 May 1987 (2 ♀), 4 June 1986 (1 ♀), 16 June 1983 (2 ♀), 20 June 1984 (1 ♀). New London Co., Voluntown, 1 km N junct. Conn. Highways 49 and 165, 15 May 1985 (1 ♀), 29 May 1986 (1 ♀). Tolland Co., Willington, 1 km SSW junct. Interstate Highway 84 and Conn. Highway 32, black spruce bog, 20 May 1986 (1 ♀), 3 June 1983 (1 ♀).

In Connecticut, adults inhabit a variety of bogs and fens bordered to some extent by woodland swamps which are the typical larval habitats (Teskey 1969). Adults have been captured between 15 May and 20 June in Connecticut. Smith et al. (1970), Golini and Wright (1978), and Leprince et al. (1983) collected adults over a 4- to 6-week period in Ontario or Quebec.

Hybomitra trepida McDunnough

Collection records.—New London Co., Colchester, 1.5 km N Conn. Highway 16 by Salmon River, 3 July 1985, canopy trap (1 ♀); Voluntown, 1 km N junct. Conn. Highways 49 and 165, 19 June 1985 (1 ♀), 16 July 1986 (1 ♀), 16–17 July 1986, horizontal Malaise trap (2 ♀).

Most specimens are from a fen surrounded by a swamp dominated by Atlantic white

cedar, *Chamaecyparis thyoides* (Linnaeus) Britton, Sterns, and Poggenburg. Like the larval habitats described by Teskey (1969) and Baribeau and Maire (1983b), the fen has abundant sphagnum. In Connecticut, adults have been taken between 19 June and 17 July. Flight periods recorded elsewhere in northeastern North America vary from 2 weeks to 2 months (Pechuman and Burton 1969, Smith et al. 1970, Lewis and Bennett 1977).

Hybomitra zonalis (Kirby)

Collection records.—Fairfield Co., Newtown, Hopewell Road by Aspetuck River, 19 June 1988, canopy trap (1 ♀). Litchfield Co., Salisbury, bog by Bingham Pond, 20 June 1984, canopy trap (2 ♀), fen by Beeslick Pond, 11–23 June 1987, horizontal Malaise trap (1 ♀), 1 km SSE Bald Peak at Wachocastinook River, 4 June 1986, canopy trap (1 ♀). New Haven Co., Guilford, Beaver Head Swamp, 7 June 1984 (2 ♀), 9 June 1984 (1 ♀), 10–11 June 1984, horizontal Malaise trap (1 ♀), 14 June 1987, on dog (1 ♀). New London Co., Voluntown, fen in Atlantic white cedar swamp by Beachdale Pond, 29 May 1985 (1 ♀), 29 May 1986, horizontal Malaise trap baited with dry ice (5 ♀), 10 June 1984 (1 ♀), 19 June 1985, horizontal Malaise trap baited with dry ice (24 ♀), 10 July 1984 (1 ♀).

Adults frequent bogs, fens, and coastal red maple swamps. Teskey (1969) and Baribeau and Maire (1983b) found larvae in Canadian bogs, fens, or both. Larvae probably develop in a wider range of habitats because collection localities in red maple swamps in Connecticut were >10 km from the nearest bog or fen. Nonetheless, based on trapping records, the largest populations of *H. zonalis* apparently occur in fens associated with coastal Atlantic white cedar swamps. Adults are on the wing at least from 29 May to 10 July, which is a comparable period in length to the one noted in Quebec by Maire (1984b). Smith et al. (1970), Lewis and Bennett (1977), and Baribeau and Maire (1983c) captured adults over a 3- to 4-week period in other areas in northeastern North America.

Stonemyia isabellina (Wiedemann)

Collection records.—New Haven Co., Hamden, Lockwood Farm, 17–18 July 1982, horizontal Malaise trap (1 ♀).

This lone female was captured in a regrowth forest that is described by Maier (1984). My specimen is the first recorded from New England. Pechuman (1981) has suggested that this species may be uncommon throughout its range. The collection date of my specimen falls within the flight period of 24 June to 31 July reported for six Pennsylvania specimens (Frost and Pechuman 1958).

Tabanus fulvicallus Philip

Collection records.—Litchfield Co., Salisbury, fen by Beeslick Pond, 18–22 July 1987, horizontal Malaise trap (1 ♀). Middlesex Co., East Haddam, bog at north end of Lake Hayward, 24 July 1985 (1 ♀).

Both collection sites have a limited number of small pools on the sphagnum mat, which resemble the areas where Teskey (1969) found larvae. The locality in Salisbury is a rich fen, and the one in East Haddam a minerotrophic bog (Maier 1988) or medium fen. Based on adult captures between 29 June and 20 July in Ontario (Pechuman et al. 1961), the flight period in Connecticut is probably brief, not exceeding 3 weeks in July.

Tabanus vivax Osten Sacken

Collection records.—Litchfield Co., Canaan, 1.2 km SSW South Canaan, 18 July 1987 (1 ♀); Cornwall, near Kellog Corners, 22 June 1988 (1 ♀); Goshen, Allyn Road, 19 July 1979 (1 ♀); Harwinton, Campville, Naugatuck River, 11 July 1985, canopy trap (1 ♀), 18 July 1987, canopy trap (2 ♀); Norfolk, 5 km S town center, 3 August 1985, canopy trap (2 ♀). Middlesex Co., East Had-

dam, bog at north end of Lake Hayward, 3 July 1984, canopy trap (1 ♀).

All localities with *T. vivax* are near streams or rivers. Teskey (1969) also emphasized the presence of streams near his larval collection sites. In Connecticut, adults fly at least from 22 June to 3 August. Pechuman et al. (1961) observed a shorter flight period of 12 June to 17 July in Ontario. Although Pechuman (1981) did not give exact dates of capture in New York, he noted that adults had been captured during June, July, and August.

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A NEW SPECIES OF CECIDOMYIIDAE (DIPTERA) DAMAGING SHOOT TIPS OF YELLOW CYPRESS, *CHAMAECYPARIS NOOTKATENSIS*, AND A NEW GENUS FOR TWO GALL MIDGES ON CUPRESSACEAE

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Abstract.—A new species of gall midge (Diptera: Cecidomyiidae) infesting the shoot tips of yellow cypress, *Chamaecyparis nootkatensis*, in British Columbia is described and illustrated. A new genus, *Chamaediplosis*, is erected for the new species and one other, previously described species, *Contarinia rugosa*, known from *Cupressus arizonica*. The new genus belongs to the tribe Cecidomyiini.

Key Words: gall midges, western North America, taxonomy

A new species is described here that was first discovered in 1987 damaging the shoot tips of yellow cypress, *Chamaecyparis nootkatensis* (D. Don) Spach (Cupressaceae) in British Columbia. The large numbers of infested and ultimately killed shoot tips at one site indicate that this species could become a serious pest (Fig. 1). The new gall midge has one generation per year at Saanichton, British Columbia. Most overwintering larvae (Fig. 2) pupate within the galls in late winter. Adults emerge soon after (Fig. 3); others pupate in the spring or early summer. Each gall usually contains one larva, but occasionally two, rarely three, are found.

A new genus is erected for the new species and *Contarinia rugosa* Gagné, another species that lives in shoot tips of Cupressaceae (Gagné 1986b). A separate paper by R. W. Duncan on the biology of the new species in British Columbia is in preparation.

METHODS

Branches with infested shoot tips were collected in the field in February, 1987 near Saanichton, B.C. To maintain the galls in fresh condition during rearing they were placed in sealed polyethylene bags and kept at a constant 20°C until adults emerged. Adults began emerging from the galls after five days and continued for several days afterwards. Immature and adult specimens were preserved in 70% ethanol and mounted for microscopic study in Canada balsam using the method outlined in Gagné (1989). Adult terminology follows usage in McAlpine (1981) and larval terminology that in Gagné (1989). The new genus is to be attributed to Gagné, the new species to Gagné and Duncan.

Chamaediplosis Gagné, NEW GENUS

Adult.—*Head:* Eyes 5–7 facets long at vertex, separated by ½ to 1 facet diameter;

facets circular, closely adjacent except near midheight of eye where they may be as far as ½ facet diameter apart. Vertex of occiput rounded, without dorsal protuberence, with 2–3 rows of setae parallel to the periphery. Frons with several setae. Labella hemispherical, with scattered setae. Palpus 4-segmented. Male antennal flagellomeres (Gagné 1986a: Fig. 1) binodal, bicircumfilar, the circumfilar loops regular. Female flagellomeres (Gagné 1986a: Figs. 2–3) progressively shorter towards antennal apex, the circumfila appressed.

Thorax: Scutum with 2 lateral and 2 dorsocentral rows of setae and setiform scales. Scutellum with a group of setae on each side. Mesanepisternum with 0–3 scales. Mesepimeron with 6–10 setae. Claws slightly shorter than empodia, the empodia broad, about as wide as 5th tarsomere. Wing with R5 curved apically to join C posterior to wing apex, C broken at juncture with R5.

Male abdomen (Figs. 4–6): Tergites 1 to 6 entire, rectangular, with mostly single, uninterrupted, posterior row of setae, 4–10 lateral setae anterior to posterior row, a few scattered scales, and pair of trichoid sensilla on anterior margin: tergite 7 as for preceding except weakly sclerotized posteromedially, posterior setae usually present only laterally; tergite 8 sclerotized only anteriorly to anterolaterally, usually bare except for anterior pair of trichoid sensilla; pleura with sparse scales; sternites 2–6 rectangular, with mostly single, caudal row of setae, with mixed setae and scales grouped near midlength, and anterior pair of trichoid sensilla; cerci broadly rounded posteriorly, with ventrolateral setae; hypoproct deeply divided, its lobes broad, rounded apically, with apical and ventral setae; aedeagus attenuate, narrowly rounded apically, with lateral sensilla; gonocoxites stout, apodeme variously shaped; gonostylus long, narrowing slightly from base to apex, mostly striate, setulae present only near base, chiefly on venter with scattered setae and completely setulose.

Female abdomen (Figs. 7–9): Tergites 1 to 7 and sternites 2–7 generally as for male, but tergal setae and scales more numerous. Tergite 7 with mostly double row of posterior setae, about ⅔ length of distal half of ovipositor; tergite 8 approximately as long as 7, with anterior pair of trichoid sensilla and 0–10 short posterior setae. Ovipositor short, protrusible, proximal half anteriorly with scattered lateral and ventral setae, distal half posteriorly with scattered short setae, completely setulose, unstriated; cerci broad at base, tapering gradually to rounded apex, completely setulose, setae concentrated at base and apex; hypoproct divided into 2 lobes.

Third instar (Figs. 10–12).—Integument rugose. Spatula present, variously shaped, with 2 anterior lobes. Papillae with basic complement of papillae for supertribe (Gagné 1989), but with very short setae; terminal papillae with short setae, the usually large, corniform pair found in Cecidomyiini reduced in size, barely larger than remaining three pairs.

Type species.—*Chamaediplosis nootkatensis* Gagné and Duncan.

Etymology.—The name *Chamaediplosis* combines "Chamae" (dwarf, creeping) from *Chamaecyparis* with "diplosis" (double, a doubling), a commonly used suffix for gall midge genera of the supertribe Cecidomyiidi.

Remarks.—*Chamaediplosis* contains *C. nootkatensis, C. rugosa,* and a third, undescribed species, known only from a series of specimens in the National Museum of Natural History in Washington, D.C. That series, from *Cupressus macrocarpa* Hartw. in California, is in poor condition and unsuitable for description. These species all infest shoot tips of Cupressaceae.

Erecting *Chamaediplosis* is a step in resolving the problem of polyphyly in *Contarinia* by dividing that genus into smaller units whose species occur on related plants and share what one can convincingly argue are shared, derived characters. *Chamaedi-*


1


2


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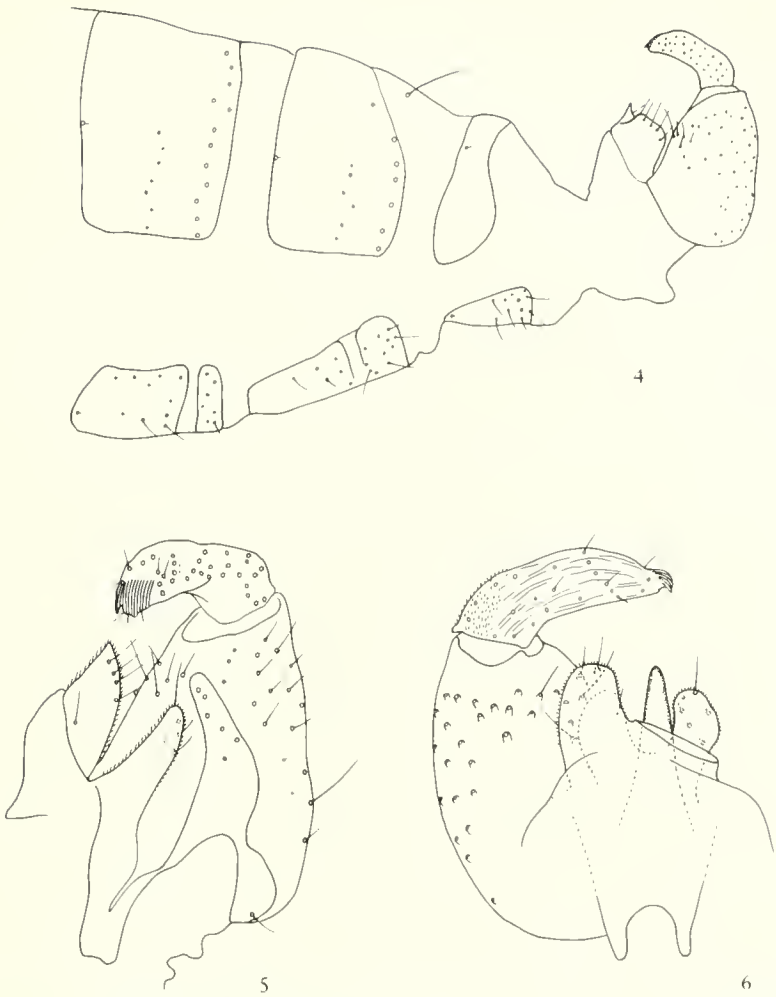
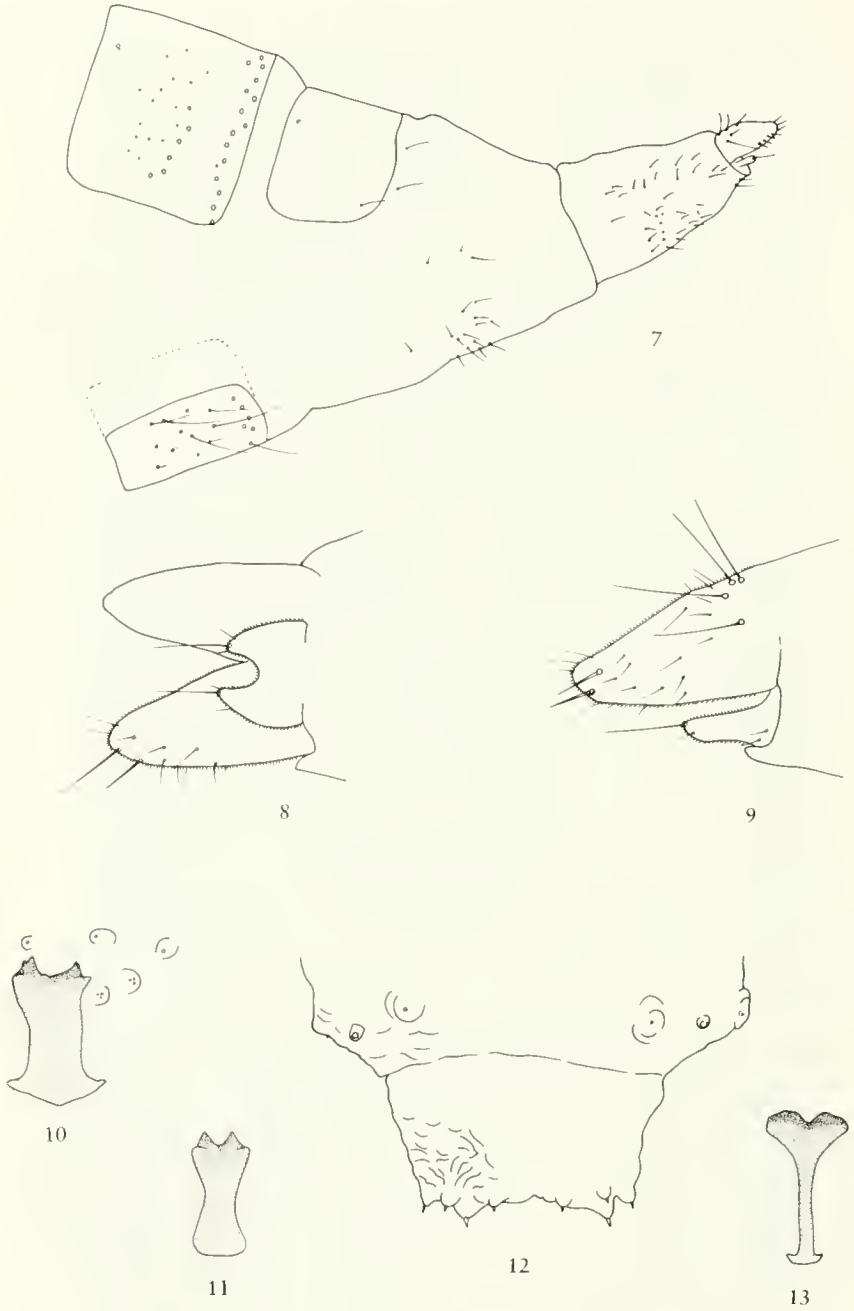


Figs. 4–6. Male, *C. nootkatensis*. 4, Abdominal segments 6 to end (lateral view). 5, Genitalia (mesal). 6, Genitalia (left side, dorsal).

plosis belongs to the tribe Cecidomyiini and differs from other genera in that tribe by its short ovipositor with relatively large and completely setulose cerci and the nearly uniform terminal papillae of the larva. That the ovipositor is short is plesiotypic, but its distinctive shape and setation (Figs. 7–9), presumably well-adapted to its use, can be regarded as apotypic. One pair of larval terminal papillae that in Cecidomyiini are much larger than the three remaining pairs and has recurved corniform setae, are in

←

Figs. 1–3. 1, Normal and infested shoot tips of yellow cypress. 2, Infested shoot tip cut open to reveal larva of *C. nootkatensis*. 3, Newly emerged female of *C. nootkatensis* and its pupal exuviae protruding from infested shoot tip.



Figs. 7–13. *C. nootkatensis*. 7–9, Female: 7, Abdominal segments 7 to end; 8, cerci and hypoproct (ventral view); 9, same (lateral). 10–12, Larva: 10, spatula with associated papillae; 11, spatula; 12, segments 8–9 (dorsal). 13, Spatula of *C. rugosa*.

Chamaediplosis only slightly larger than that of the remaining papillae. Its small size may be a reduction or, alternatively, the primitive condition for the tribe.

Except for the shape of the ovipositor and the larval terminal papillae, *Chamaediplosis* could fit into *Contarinia*, a genus that is used as a catch-all category and has grown to include most species of Cecidomyiini with elongate, strongly tapered ovipositors (Gagné 1973). It now appears that long ovipositors suitable for laying eggs in narrow crevices of buds and flowers evolved separately many times (Gagné 1989). One conspicuous similarity between the new genus and *Contarinia* is the loss of one of the three circumfila on the male antennal flagellomeres. That is a character state that appears many times within the Cecidomyiini and is not necessarily evidence for particularly close kinship. The number of circumfila has become reduced separately elsewhere in the Cecidomyiini (*Taxodiomyia*), as well as in the Clinodiplosini (*Ametrodiplosis*), Lestodiplosini (*Endaphis, Dentifibula*), and Mycodiplosini (*Mycodiplosis*: Gagné and Rios de Saluso 1987). Other apotypic character states besides the bicircumfilar flagellomeres that *Chamaediplosis* and some other Cecidomyiini share but which may be the result of convergence are 1) the loss of the dorsal occipital projection of the head, 2) a certain amount of reduced setation and sclerotization in male abdominal tergites 7 and 8, 3) the deeply divided hypoproct with 2 short, cylindrical lobes, 4) the short aedeagus, 5) the presence of setulae only at the base of the gonostylus, and 6) the large empodia. The last is a character that this genus shares with most other conifer gall midges, regardless of their affinities.

Key to Species of *Chamaediplosis*

Larvae and pupae in shoot tips of *Chamaecyparis nootkatensis*; larval spatula with triangular anterior lobes, occasionally the lobes secondarily toothed, the shaft slightly narrowed near midlength (Figs. 10–11); female tergite 8 with 0–5 setae along posterior margin (Fig. 7); aedeagus acute at apex (Fig. 6) . . . . . *C. nootkatensis* Gagné and Duncan

Larvae and pupae in shoot tips of *Cupressus arizonica*; larval spatula with rounded anterior lobes, the shaft much narrowed posteriorly (Fig. 13); female tergite 8 with 10–12 setae along posterior margin; aedeagus broadly rounded at apex . . . . . *C. rugosa* Gagné

Chamaediplosis nootkatensis Gagné and Duncan, New Species

Adult.—Wing length, 2.0–2.5 mm. Thorax: anepisternum usually with 0, occasionally 1 scale; anepimeron with 6–9 setae. Male postabdomen as in Fig. 4, genitalia as in Figs. 5–6, the apodeme variable, bifurcate (as shown, Fig. 7) or entire. Female postabdomen as in Fig. 7, cerci and hypoproct as in Figs. 8–9.

Third instar.—Orange. Spatula (Figs. 10–12) short and broad, anteriorly with two triangular lobes, these sometimes secondarily divided. Papillae all on mamelons. Posterior segments as in Fig. 12.

Holotype.—Male, ex *Chamaecyparis nootkatensis*, Saanichton, British Columbia, III-3-1987, R. Duncan, deposited in the Canadian National Collection in Ottawa. Paratypes, all ex *Chamaecyparis nootkatensis* from Saanichton, B. C.: 2 males, 2 females, II-23-1987; 2 males, 1 female, III-3-1987; 4 males, 3 females, III-10-1987; 5 males, 2 females, IV-22-1988; and 5 larvae, IV-11-1987. The paratypes are divided among the U.S. National Museum of Natural History, Washington, D.C., the Pacific Forestry Centre, and the Canadian National Collection.

Remarks.—Except in the shape of the larval spatula, this species is very similar to *C. rugosa*. Adults of the two species can be separated with the help of the minor differences outlined in the key given earlier.

Acknowledgments

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REVIEW OF *HALTICHELLA* SPINOLA IN THE NEARCTIC REGION (HYMENOPTERA: CHALCIDIDAE)

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Abstract.—Five species of *Haltichella* Spinola are recognized in the Nearctic region: *H. onatas* (Walker), *H. ornaticornis* Cameron, *H. perpulcra* (Walsh), *H. rhyacionia* Gahan, and *H. xanticles* (Walker). The females and males of each species are diagnosed. A neotype is designated for *H. perpulcra*. The males of *H. onatas, H. ornaticornis, H. perpulcra,* and *H. xanticles* were previously undescribed; voucher specimens of each are designated. Biological and distributional information is summarized for each species. A key to the Nearctic species and characters to distinguish *Haltichella* from other Nearctic Chalcididae are presented.

Key Words: *Haltichella,* review, Chalcididae, Nearctic

Haltichella Spinola is one of fifteen genera of Chalcididae in America north of Mexico and is known from all zoogeographical regions. This genus was described by Spinola (1811) with *Chalcis pusilla* Fabricius as the type-species. Taxonomic treatments of *Haltichella* include the European fauna (Boucek 1951), the Russian fauna (Nikolskaya 1952, 1960), the African fauna (Schmitz 1946), and the Japanese fauna (Habu 1960, 1962). As no comprehensive taxonomic work for the Nearctic species exists, I present a review of Nearctic *Haltichella.* Past literature on *Haltichella* is cataloged in Peck (1963), Burks (1979), and DeSantis (1979).

Haltichella are among the smallest Chalcididae, length rarely exceeding 4 mm. They are black and commonly with orange or orange-brown on the legs, antennae, and rarely, the tegulae. The wings vary, being hyaline, smokey, or clouded in a specific pattern. Males differ from females by having a shorter abdomen with a blunt apex (Fig. 2), robustly filliform antennae (Fig. 3), and in some species, in color and forewing clouding.

A generic revision of the American Chalcididae is in progress (Boucek pers. comm.); therefore, a generic description of *Haltichella* is omitted. However, to facilitate identification of this genus for the Nearctic region, the following characters are diagnostic (Fig. 1):

> hindtibia truncate distally, two spurs present (Haltichellinae); marginal vein reaching anterior margin of wing, postmarginal and stigmal veins present (Haltichellini); tergite 1 dorsally with longitudinal carinae at base, originating from a transverse carina; scutellum rounded, slightly bilobed, or rarely, strongly bilobed posteriorly but never with large, long projecting processes or a median tooth; vertex of head not produced into horns; frontal carina weak, not forming an arch above anterior ocellus; color predominantly black.

Useful species characters include the length of tergite 2 (medially); sculpture of tergite 1 (dorsally); color of the antennae, tegulae, and legs (especially the hindfemur); and presence or absence of clouding in the forewing. Besides the above characters, few diagnostic and constant characters exist to distinguish the Nearctic species. Rarely, individual specimens are difficult to identify because of variation in the sculpture of tergite 1 and coloration. If possible, a series of specimens from a locale should be examined. However, more than one species can be taken together such as *Haltichella rhyacionia* Gahan and *Haltichella xanticles* (Walker).

Haltichella are primary parasitoids of Lepidoptera, secondary parasitoids of braconid wasps, and once recorded as a secondary parasitoid of a tachinid fly (Freeman and Berisford 1979). Four of the five Nearctic species have been reared with three species being both primary and secondary parasitoids and the fourth species as only a secondary parasitoid. Primary hosts include several economically important lepidopterous pests (see host sections). During this revision, many new host records were obtained from label data.

In the examination of several thousand specimens, the distributional information on *Haltichella* was greatly improved and shows the species to be widely distributed in the Nearctic region (Fig. 5). *Haltichella* are commonly collected in Malaise-type traps and pan traps or by sweeping vegetation. Some species (e.g. *H. xanticles*) occur in a variety of habitats, ranging from deserts to coniferous forests. *Haltichella* are common in collections, ranking third in number only to the Chalcididae genera *Spilochalcis* and *Invreia*.

Abbreviations include T1 for tergite 1, etc. All measurements were made in the flattest plane possible. Specimens were examined at 30 to 100×. A mylar, glare reducing screen was used in lighting specimens.

Collections examined and museum acronyms are as follows: American Museum of Natural History, New York; Bernice P. Bishop Museum, Hawaii; British Museum of Natural History, London (BMNH); California Academy of Sciences, San Francisco; California Collection of Arthropods, California Department of Food and Agriculture, Sacramento; California State University, Fresno; California State University, Sacramento; Canadian National Collection, Ottawa; Florida Collection of Arthropods, Florida Department of Agriculture and Consumer Affairs, Gainesville; Fresno County Department of Agriculture, Fresno, California; Illinois Natural History Survey, Champaign; Los Angeles County Museum of Natural History, California; Natural History Museum of San Diego, California; Oregon Department of Agriculture, Salem; Royal Ontario Museum, Toronto; Texas A&M University, College Station; Tulare County Agricultural Commissioner's Office, Visalia, California; United States National Museum of Natural History, Washington, D.C. (USNM); University of California, Berkeley; University of California, Davis; University of California, Riverside; J. A. Halstead personal collection; H. A. Hespenheide personal collection; R. D. Haines personal collection.

Key to Nearctic Species of *Haltichella* Spinola

1. Females, ovipositor present 2
– Males, ovipositor absent 6
2. T2 medially less than ¼ the length of T1 ..... *perpulcra* (Walsh)
– T2 medially greater than ¼ the length of T1 .. 3
3. T1 punctate to coriaceous dorsally ..... *rhyacionia* Gahan
– T1 polished dorsally, without sculpture 4
4. Forewing with one or two clouded spots, rarely hyaline; tegula orange, hindfemur black or with only apex orange ..... *ornaticornis* Cameron
– Forewing hyaline, tegula black, hindfemur not as above 5
5. Legs and antennae black, forewing hyaline or smokey ..... *xanticles* (Walker)
– Legs (except apical ½ of hindfemur occasion-

ally) and antennae orange, forewing hyaline ..... *onatas* (Walker)

6. T1 basally with 2 longitudinal carinae, flagellum 2½× height of head ..... *perpulcra* (Walsh)
– T1 basally with 3 or more longitudinal carinae, flagellum less than 2½× height of head 7
7. T1 punctate to coriaceous dorsally ..... *rhyacionia* Gahan
– T1 polished dorsally, without sculpture .. 8
8. Tegula orange, rarely black; forewing with one or two clouded spots, rarely hyaline ..... *ornaticornis* Cameron
– Tegula black, forewing hyaline or smokey but never with a clouded spot 9
9. Hindfemur with basal ⅕ to ½ orange, fore and middle legs and scape orange ... *onatas* (Walker)
– Hindfemur black, or with orange markings at base and/or apex; fore and middle legs and scape black or brown .. *xanticles* (Walker)

Haltichella onatas (Walker)
Fig. 5

Hockeria onatas Walker, 1843: 146, ♀.
Haltichella onatas (Walker); Walker, 1846: 7.
Conura onatas (Walker); Walker, 1871: 41.
Haltichella longicornis Ashmead, 1887: 185; Burks, 1975: 164.
Haltichella onatas (Walker); Burks, 1975: 164, Lectotype designation.
Haltichella onatas (Walker), MALE DIAGNOSIS.

Diagnosis.—*H. onatas* is the only Nearctic species with the antennae (in male scape only) and legs (in male only basal ⅕ to ½ of hindfemora and apex of hindtibiae) orange. The characters: length of T2 medially greater than ¼ that of T1, T1 dorsally polished, with three or more (usually) longitudinal carinae at base, hyaline forewing, black tegulae, and orange color are distinguishing.

Female.—Black, with antennae and legs orange to orange-brown.

Male.—Like female except antennae robustly filiform, base of hindfemora and apex of hindtibiae orange, and abdomen shorter with apex blunt.

Variation.—Hindfemur coloration is somewhat variable as noted in the key. (♀) Length 2–4 mm. The hindfemur of one female (Type No. 2627 U.S.N.M., originally included in the syntype series of *H. xanticles*) is black, except basally. (♂) Length 2–3 mm.

Type and voucher specimens.—Lectotype ♀ with data: "B.M. Type Hym. 5. 553, I477a, St. Jon's Bluff, *Hockeria Onatas* Walker." I designate a male specimen as a voucher specimen—red label marked: "VOUCHER MALE, *Haltichella onatas* (Walker), ♂, det. J. A. Halstead 1987" and with data: "Crescent City, Fla. Apr' 08, Van Duzee, MCVanDuzee Collector, MCVanDuzee Collection, Collection of the CALIFORNIA ACADEMY OF SCIENCES, San Francisco, Calif." Both specimens in the United States National Museum.

Hosts.—LEPIDOPTERA, Cosmopterygidae: *Pyroderces rileyi* (Wals.). Olethreutidae: *Lasperyresia pomonella* (L.) pupa, *Grapholitha molesta* (Busck). Gelechiidae: *Isophrictis similiella* (Chamb.). Psychidae: *Prochalia pygmaea* Barnes & McDunnough. A specimen (New Orleans, Louisiana) was reared from a leaf skeletonizer on *Phalaris canariensis* (Canary Grass). Ashmead (1887) reared a specimen from the gall of *Xanthoteras politum* (Bassett) (Hymenoptera: Cynipidae). It is likely that a lepidopteran was inhabiting the gall. A specimen (Monticello, Florida) was reared from a stalked braconid wasp cocoon on *Catocala* (Lepidoptera: Noctuidae); thus, it is also a secondary parasitoid of Braconidae.

Haltichella ornaticornis Cameron
Fig. 5

Haltichella ornaticornis Cameron, 1884: 100, ♀.
Haltichella ornaticollis Cameron; Howard, 1885: 36.
Haltichella ornaticornis (Cameron); DeSantis, 1979: 69.
Haltichella ornaticornis Cameron, MALE DIAGNOSIS.

Diagnosis.—*H. ornaticornis* is the only Nearctic species with one or two clouded

spots in the forewing. The characters: length of T2 medially greater than ¼ that of T1, T1 dorsally polished, with three or usually more longitudinal carinae at base, orange tegulae, black hindfemora, orange and black antennae (in female), and black antennae (in male) are distinguishing.

Female.—Black, with the following areas orange: basal ½ of scape, flagella 1–3, tarsi, base and apex of tibiae, trochanters, and tegulae. Forewing with a clouded spot from under marginal vein and stigma to middle of wing.

Male.—Like female except antennae black and robustly filiform, and abdomen shorter with apex blunt. Forewing like female.

Variation.—(♀) Length 2–4 mm. Forewing clouding somewhat variable. Most specimens are like the holotype, but some with forewing hyaline or with two clouded areas (one under the marginal vein and another fainter spot between it and apex of wing). (♂) Length 2–3 mm. Commonly, the forewing is hyaline. The tegulae are rarely black.

Comments.—Females that lack forewing clouding can be distinguished by coloration and T1 and T2 characters.

Type and voucher specimens.—Holotype ♀ with data: "Bugaba, Panama, Champion. BM Type Hym. 5. 288, *Haltichella ornaticornis* Cameron." I designate a male specimen as a voucher specimen—red label marked: "VOUCHER MALE, *Haltichella ornaticornis* Cameron, ♂, det. J. A. Halstead 1987" and with data: "MEXICO, Chiapas, Palenque, 10 Sept 1974, GBohart, WHanson, UTAH STATE UNIVERSITY." Both specimens in the British Museum of Natural History.

Host.—Unknown.

Haltichella perpulcra (Walsh)
Figs. 4, 5

Hockeria perpulcra Walsh, 1861: 258, ♀. (Paper not seen by author.)

Hockeria perpulchra Walsh; Cresson, 1862: 228 (erroneous subsequent spelling).

Conura perpulchra (Walsh); Walker, 1871: 41.

Hockeria perpulcra Walsh; Thomas, 1881: 39, Original description repeated.

Haltichella perpulchra (Walsh); Howard, 1885: 37.

Haltichella perpulcra (Walsh), NEOTYPE DESIGNATION ♀, MALE DIAGNOSIS.

Diagnosis.—*H. perpulcra* is the only Nearctic species with the length of T2 medially less than ¼ that of T1 (Fig. 4), and (in male) flagellum 2½× the height of head. The characters: hyaline forewing, T1 dorsally polished, with two longitudinal carinae at base (in both sexes) and between these carinae 0–5 minute carinae (in female), and black color are distinguishing.

Female.—Black, with base and apex of fore and middle tibiae, apex of hindtibiae, and tarsi orange.

Male.—Like female except antennae longer and robustly filiform, and abdomen shorter with apex blunt.

Variation.—(♀ and ♂) Length 2–4 mm.

Type and voucher specimens.—The type specimen(s) could not be found and are believed to have been destroyed in the Chicago fire of 1873. I was unable to obtain Walsh's (1861) paper of the original description. Thomas (1881), republishing Walsh's (1861) description, presented key characters: "abdomen ovate, glabrous, first joint equal to three-fifths of its entire length, and highly polished, intermediate joints very narrow," "wings hyaline," and "general color black" (in combination with other characters in the description), which are adequate to distinguish this species. Walsh's description appears to have been based on a female. I designate a female specimen as NEOTYPE—yellow label marked: "NEOTYPE, *Haltichella perpulcra* (Walsh), ♀, det. J. A. Halstead 1987" and with the data: "MEXICO, Nyarit, San Blas, II-14-1974, G. E. Bohart, UTAH STATE UNIVERSITY." I designate a male specimen as a voucher specimen—red label marked:

"VOUCHER MALE, *Haltichella perpulcra* (Walsh), ♂, det. J. A. Halstead 1987" and with data: "MEXICO, Chiapas, Palenque, 10 Sept 1974, GBohart, WHanson, UTAH STATE UNIVERSITY." Neotype and voucher specimen of male deposited in the USNM.

Host.—Cocoons of *Apanteles militaris* (Walsh) (Hymenoptera: Braconidae) on *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae).

Haltichella rhyacionia Gahan
Figs. 1–3, 5

Haltichella rhyacioniae Gahan, 1927: 545, ♀ and ♂.
Haltichella rhyacionia Gahan; Burks, 1979: 861.
Haltichella rhyacionia Gahan, MALE DIAGNOSIS.

Diagnosis.—*H. rhyacionia* is the only Nearctic species with T1 dorsally coriaceous to punctate. The characters: length of T2 medially greater than ¼ that of T1 (Figs. 1–2), T1 with three or usually more longitudinal carinae at base, hyaline forewing, and black legs and tegulae are distinguishing.

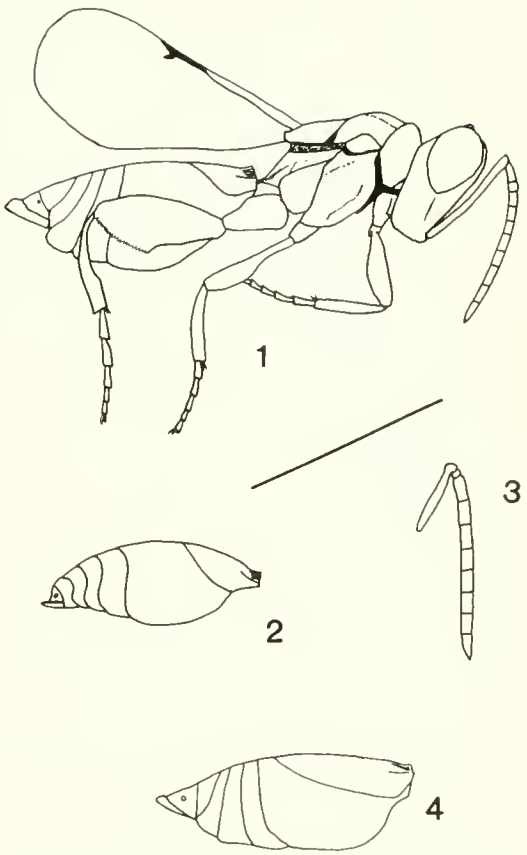
Female.—Black, with apices of tibiae orange.

Male.—Like female except antennae robustly filiform and abdomen shorter with apex blunt.

Variation.—(♀ and ♂) Length 2–4 mm. T1 coriaceous to punctate. The sculpture on T1 dorsally is rarely faint and confined to the basomedial area. The flagellum is rarely orange.

Types.—Holotype ♀ and allotype ♂ in USNM with data: "ex *Rhyacionia frustana* Comst, Falls Ch Va, 7/16/24, R. A. Cushman coll., Type No. 40178 U.S.N.M., *Haltichella rhyacioniae* Gahan Type."

Hosts.—LEPIDOPTERA, Olethreutidae: *Rhyacionia bushnelli* (Busck), *R. frustrana, R. rigidana* (Fern). Lyonetiidae: *Bucculatrix thurberiella* (Busck). DIPTERA, Tachinidae: *Lixophaga mediocris* Towns.



Figs. 1–4. *Haltichella rhyacionia* Gahan. 1, Habitus of female. 2, Abdomen of male (lateral view). 3, Antenna of male (lateral view). 4, Abdomen of *Haltichella perpulcra* female (lateral view). Scale line 1.5 mm.

Haltichella xanticles (Walker)
Fig. 5

Hockeria xanticles Walker, 1843: 147, ♀.
Haltichella xanticles (Walker); Walker, 1846: 7.
Conura Xanticles (Walker); Walker, 1871: 41.
Haltichella americana Howard, 1885: 36; Burks, 1975: 165.
Haltichella xanticles (Walker); Burks, 1975: 165, Lectotype designation.
Haltichella xanticles (Walker), MALE DIAGNOSIS.

Diagnosis.—*H. xanticles* is similar to *H. rhyacionia*, but differs in coloration and the

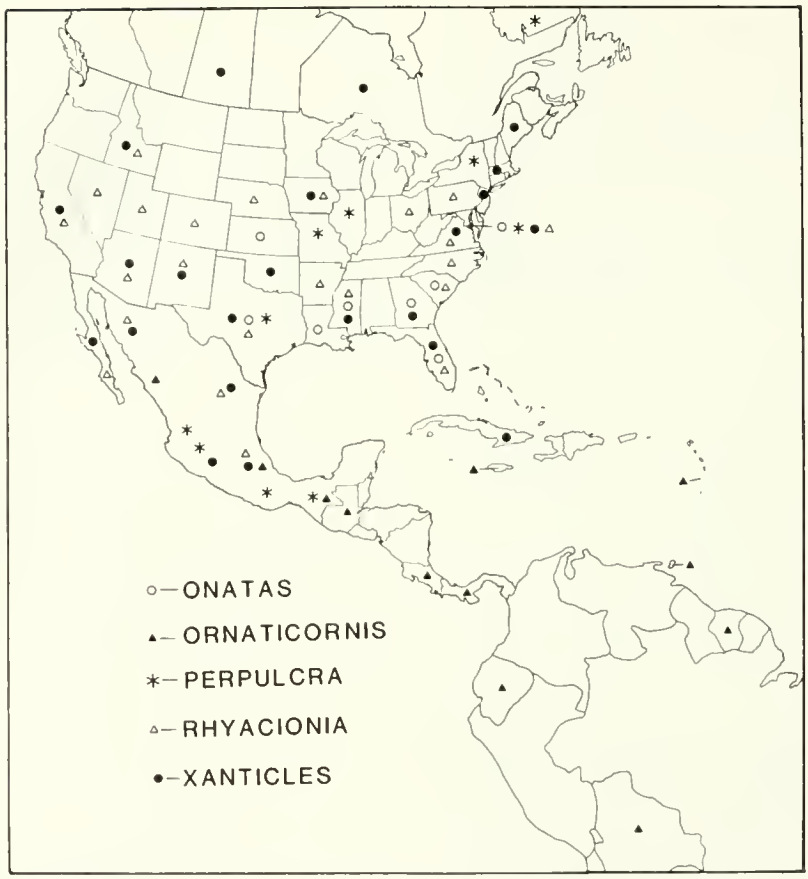


Fig. 5. Distribution of Nearctic species of *Haltichella*. One species' range includes the Neotropical region. A symbol in a state, province, or country indicates the species is widely distributed in that region.

sculpture of T1 dorsally. The characters: length of T2 medially greater than ¼ that of T1, T1 dorsally polished, with three or usually more longitudinal carinae at base, hyaline forewing, and black tegulae and legs are distinguishing.

Female.—Black, with base and apex of fore and middle tibiae, apex of hindtibiae, and tarsi orange.

Male.—Like female except antennae robustly filiform and abdomen shorter, with apex blunt.

Variation.—(♀ and ♂) Length 2–4 mm. The hindfemur is rarely dark red-brown.

Type and voucher specimens.—Lectotype ♀ with data: "B.M. Type Hym. 5.554, 1478a, St. Jon's Bluff, *Hockeria Xanticles* Walker." I designate a male specimen as a voucher specimen—red label marked: "VOUCHER MALE, *Haltichella xanticles* (Walker), ♂, det. J. A. Halstead 1987" and with data: "Mill Valley, Marin Co., Cal., 2. VII. 50, H. B. Leech Collector, Collection of the CALIFORNIA ACADEMY OF SCIENCES, San Francisco, Calif." Both specimens in the USNM.

Hosts.—LEPIDOPTERA, Lymantriidae: *Lymantria dispar* (L.). Olethreutidae: *Rhyacionia buoliana* (Schiff.), *Rhyacionia* sp., *Grapholitha molesta*. Gelechiidae: *Exoteleia pinifoliella* (Chamb.). Coleophoridae: *Coleophora laricella* (Hbn.). Lyonetiidae: *Bucculatrix canadensisella* (Chamb.). Psychidae: *Solenobia walshella* Clem. Pyralidae: *Dioretria disclusa* Heinr. HYMENOPTERA, Braconidae: *Cotesia melanoscelus*

(Ratzeburg). Label data on one specimen (Texas, Westaco) indicates emergence with *Antonina graminis* (Mask.) (Homoptera: Pseudococcidae) from a breeding cage. Another specimen (Maine, Mtn. Desert Is.) was bred from a parasite of *Coleophora salmani* Heinr. (Coleophoridae).

Acknowledgments

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ISOZYME ANALYSIS IN SIX POPULATIONS OF *PEDIOBIUS FOVEOLATUS* (CRAWFORD) (HYMENOPTERA: EULOPHIDAE)

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Abstract.—Sixteen enzyme loci were used to determine the degree of genetic variability and taxonomic status of *Pediobius foveolatus* (Crawford) (a hymenopterous parasite of *Epilachna* spp.) from Japan, Korea, China, Hong Kong, Guam, and India. Two loci, ACON-1 and MDH-1 were found to be polymorphic. However, no intra-population variation was found for any of the 16 loci studied. Based on these isozyme analyses, three biotypes were recognized in *P. foveolatus*, namely, the China biotype with its unique ACON-1 genotype, the Northern biotype with MDH-1^s allele, and the Southern biotype with MDH-1^f allele.

Key Words: allelic repression, biotype, electrophoresis, *Epilachna*

Pediobius foveolatus (Crawford) is a gregarious parasite of larvae of *Epilachna* spp. (Coleoptera: Coccinellidae). It is found naturally in widespread areas of the Asiatic, Australasian, and African regions (Kerrich 1973). In recent years it has been reported in Japan (Tachikawa 1976), Sumatra (Abbas and Nakamura 1985), and China (Schaefer et al. 1986). Recent collections have recovered it in South Korea and in Hong Kong (Schaefer, unpubl. data).

In the early 1950's, under the name *Pleurotropis epilachnae* Rohwer, this parasite was intentionally introduced into Guam from the Philippines to combat the introduced *Epilachna philippinensis* Dieke (Peterson 1955). It was introduced into North America from Bangalore, India, for the control of Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, in 1966 (Angalet et al. 1968). It failed to overwinter in the U.S. but has repeatedly shown promise as it readily attacks MBB larvae during the season of its release. In the belief that a race from temperate areas might be capable of surviving winters in North America, one of us (P.W.S.) obtained *P. foveolatus* (hereafter referred to as *Pediobius*) from Honshu, Japan, and first released it in North America in 1980 but this race also did not permanently establish (Schaefer et al. 1983). We have concluded that *Pediobius* probably requires an alternate host *Epilachna* sp. which overwinters as a larva or pupa. In parts of Asia there are some species with this trait. The only three species in the Epilachninae in the eastern U.S. all overwinter as adults.

At the time of the release of the Japanese *Pediobius*, we attempted to distinguish this race from the Indian one which, at the time, was being released in widespread projects in several mid-Atlantic states (thus necessitating our releases in the Mississippi River valley). Being unable to distinguish these two races morphologically, we turned to electrophoretic analysis to provide a marker

Table 1. History of cultures of *Pediobius foveolatus* at BIRL.

Designation	Locality	Date of Receipt	Starter Sample Size	No. Generation in Laboratory
Japan (A)	Kurashiki, Honshu	8/15/79	2878 M&F[a]	131
Japan (B)	Yashiro, Honshu	8/27/80	1497 M&F	108
Korea	Seoul	10/04/82	259 M&F	63
China	Beijing & Taiyuen	11/07/84	3M, 79F	23
Hong Kong	Fanling, New Territory	8/05/82	2271 M&F	44
	Fanling, New Territory	8/06/83	352 M&F	
Guam	Mangilao	6/24/85	18M, 86F	11
India (A)	Devanahalli, Bangalore	5/24/72[b]	398 M&F	286[d]
	Avali, Bangalore	7/5–8/21/73[c]	2814 M&F	
India (B)	Re-colonized subculture from (A) (Same as above)			286[d]

[a] M = males, F = females.
[b] Only one of four 1972 shipments (with about 30 females) contributed to the laboratory culture.
[c] Four shipments including 1596 females.
[d] Approximate generation number based on calculations.

which might identify the Japanese population. As more races became available, we extended this study into an assessment of the genetic heterozygosity of *Pediobius* from widely scattered geographical locations (Japan, Korea, China, Hong Kong, India, and Guam) as well as some of the inter-cross races maintained in culture at Beneficial Insects Research Laboratory (BIRL), Newark, Delaware. We report on the electrophoretic means of distinguishing some populations from others and on the overall genetic heterozygosity of this species based on reared material which originated from the locations given.

Materials and Methods

Living material was obtained from cultures being reared at BIRL. The origin and brief history of each culture, date(s) of importation, starter sample size, and the generation number (or approximation) of each culture are presented in Table 1. The ultimate rearing procedure was to maintain each culture in unwaxed paper cups (112 mm ID at top, 55 mm deep, capacity 470 ml) with clear plastic lids. Sting units were set up approximately every two to three weeks by aspirating ca. 20–30 adults (ca. equal sex ratio) from old cups and expelling them into new cups which contained 25 fourth instar MBB larvae. These sting units sat for ca. 6 h, after which all *Pediobius* were collected by aspiration and destroyed. Care was taken never to return specimens into cups once they were removed or escaped. This was done as a precaution to prevent any genetic mixing of indistinguishable wasp strains. The host larvae were then transferred to reusable rigid polyethylene cylindrical cages (158 mm ID, 120 mm deep) with three fine mesh screen portals (5 cm dia.) on the sides for air circulation and inverted glass pie plates for covers. Food was provided as a bouquet of Tendergreen snapbean plants in a glass vial of water with cotton plugging firmly holding the plant stems. Food was replaced during the first week if needed. During the second week host larvae were transferred into new paper cups to await adult emergence. Just prior to expected emergence (two to three weeks depending on the seasons since ambient indoor temperature and humidity was not regulated), the inner surface of the lid was smeared with honey as the only food source. Water was not usually provided but on occasion if drying was evident, water was injected through the cup wall using a hypodermic needle.

Material used in the electrophoretic analysis was taken from the cup after a subsam-

Table 2. Gel and electrode buffer systems.

Designation	Description	Source
MC	N-(3-Aminopropyl)-morpholine-citrate (pH 6.0)	Clayton and Tretiak (1972)
PK	Discontinuous Tris-citrate (Electrode: pH 8.2; Gel: pH 8.7)	Poulik (1957)
TC	Tris-citrate (pH 7.0)	Siciliano and Shaw (1976)
TVB	Tris-versene-borate (pH 8.0)	Siciliano and Shaw (1976)

ple was removed to begin the next generation. Specimens in their intact paper cups were shipped or hand-carried to Beneficial Insects Laboratory (BIL), Beltsville, Maryland, and samples were then frozen and stored at −65°C until electrophoresis.

Electrophoretic Methods

Electrophoresis was performed on horizontal starch gels for 4 h using 6% Electrostarch, 6% Sigma starch, 5% sucrose, 10 mg NADP, and 400 ml gel buffer (see Table 2). The 12 enzyme systems examined are listed in Table 3, each followed by the buffer systems used. At least six female and six male wasps per enzyme per culture were electrophoresed. Sample sizes were increased to over 20 for loci that exhibited polymorphisms. At least 18 female progeny were used in the controlled progeny analyses of genotypes at ACON-1 and MDH-1 loci.

We assumed that discrete zones of enzyme activity were controlled by single loci coding for specific products. The genetic basis of observed isozyme variations (see ACON and MDH below) were confirmed by progeny analyses. Loci coding for the same enzyme are numbered sequentially from the most anodal to the most cathodal regions of activity. The allelic proteins are designated alphabetically, with "A" the fastest running allele. The allelic designations in ACON-1 and MDH-1 were inferred from progeny analyses and were labelled as "F" or "S."

Results and Discussion

In addition to the enzymes shown in Table 4, we also examined acid phosphatase, aldehyde oxidase, esterase, galactose-6-phosphate dehydrogenase, glutamate dehydrogenase, leucine aminopeptidase, and superoxide dismutase. However, these enzymes had either very weak or streaky bands

Table 3. Enzymes analyzed in *P. foveolatus*, with buffer conditions employed.

EC* no.	Enzyme	Buffer System
4.2.1.3	aconitase (ACON)	MC
1.1.1.49	glucose-6-phosphate dehydrogenase (G6PD)	MC
2.6.1.1	glutamate-oxaloacetate transaminase (GOT)	MC
1.1.1.8	alpha-glycerophosphate dehydrogenase (GPDH)	TC, TVB
2.7.1.1	hexokinase (HK)	PK, TVB
1.1.1.42	isocitrate dehydrogenase (IDH)	TC
1.1.1.27	lactate dehydrogenase (LDH)	TC
1.1.1.37	malate dehydrogenase (MDH)	MC, TC
1.1.1.40	malic enzyme (ME)	TC
1.1.1.44	6-phosphogluconate dehydrogenase (6PGD)	MC
5.3.3.9	phosphoglucose isomerase (PGI)	MC, TC
2.7.5.1	phosphoglucomutase (PGM)	MC, PK

* Enzyme Commission.

Table 4. Isozyme phenotypes of six *Pediobius foveolatus* populations.

Enzyme locus	Population**					
	Japan	Korea	China	Hong Kong	Guam	India
ACON-1	FF	FF	SS	FF	FF	FF
ACON-2	AA	AA	AA	AA	AA	AA
GOT	AA	AA	AA	AA	AA	AA
G6PDH	AA	AA	AA	AA	AA	AA
GPDH-1	AA	AA	AA	AA	AA	AA
GPDH-2	AA	AA	AA	AA	AA	AA
HK-1	AA	AA	AA	AA	AA	AA
HK-2	AA	AA	AA	AA	AA	AA
IDH	AA	AA	AA	AA	AA	AA
LDH	AA	AA	AA	AA	AA	AA
MDH-1	SS	SS	FF	FF	SS	FF
MDH-2	AA	AA	AA	AA	AA	AA
ME	AA	AA	AA	AA	AA	AA
PGM	AA	AA	AA	AA	AA	AA
PGI	AA	AA	AA	AA	AA	AA
6PGD	AA	AA	AA	AA	AA	AA

** Japan (A) and Japan (B) were combined as there were no differences between them. India (A) and India (B) were also combined for the same reason.

that could not be clearly scored. Therefore, only data on 12 enzyme systems were used in this analysis (Table 4).

All the enzymes in this study migrated anodally with the buffer conditions employed except ACON-2, MDH-2 and 6-PGD which migrated cathodally (MDH-1 and MDH-2 also migrated cathodally in the MC buffer). Only four enzyme systems had more than two loci and with the exception of ACON-1 and MDH-1, all other loci were monomorphic (Table 4). Progeny analyses also revealed that ACON is monomeric and MDH is dimeric in *Pediobius*.

Although the five populations we studied were identical at 14 loci, there are some differences at the other two loci. As shown in Table 4, two alleles were found at both ACON-1 and MDH-1 with each population fixed for one of the two alleles at each locus. The China population was unique in being fixed for the slow allele at ACON-1 while the others were fixed for the fast allele at this locus. Guam, Japan, and Korea populations were fixed for the MDH-1^s allele while samples from China, Hong Kong, and India were fixed for the MDH-1^f allele.

Although Hung et al. (1986) reported high levels of genetic heterozygosity in the hyperparasitic wasp, *Mesochorus nigripes*, very low levels of electrophoretic variation have been found in most hymenopteran species. Some species even lack variation altogether (Wagner and Briscoe 1983). The genetic homogeneity found within each population at these 16 loci possible is not the result of founders effects, because even the smallest sample (China culture) originated from 79 female wasps collected from two widely separated localities. This lack of enzyme variation might be due to inadvertent selection during long periods of laboratory rearing as in the case of the screwworm fly (Bush et al. 1976). Since the starter materials were not analyzed electrophoretically, the validity of this assumption cannot be ascertained.

Pleurotropis epilachnae, described as a separate species from India by Rohwer, was synonymized under *Pediobius foveolatus* (Crawford) by Kerrich (1973), because the differences in size and color did not hold up in specimens other than the type series. Therefore, our samples were all identified as *P. foveolatus* and no morphological differences were found among them (M. E. Schauff, pers. comm.).

According to Peterson (1955), *Pleurotropis epilachnae* Rohwer (= *P. foveolatus*) was successfully introduced into Guam from the Philippines during 1954 to control the phytophagous ladybeetle, *Epilachna philippinensis* Dieke. The BIRL quarantine records also show that the only recorded shipments to Guam occurred in 1974 (three shipments) and 1975 (three shipments) and are recorded as origin "India." The Japan culture was first obtained in August 1979, and has never knowingly been imported into Guam. Therefore, it is rather puzzling that the Guam population was the same as the Japan and Korea populations in having only

the slow allele at MDH-1. Over 30 female wasps from the Guam culture analyzed all had only the slow allele and it is not likely that this culture was contaminated. We cannot explain the apparent contradiction between our findings and the implications based on historical records.

Our cultures of these six populations crossed successfully in both directions under laboratory conditions. Peng (1988) also reported that there was no reproductive isolation between his Beijing *Pediobius* and those from Hong Kong, India, Japan, and Korea that he received from PWS. However, he reported that "malic dehydrogenase (sic)" was one of three enzymes that were monomorphic in the five cultures he studied. This is different from our results as shown in Table 4. It is possible that the lack of variability in his malate dehydrogenase study is due to the poor resolution of the buffer system and supporting medium he used (see Hung and Vinson 1977).

Four patterns of allelic repression have been reported in interspecific as well as intertribal hybrids (Avise and Duvall 1977, Hung and Vinson 1977): (a) repression of paternal protein synthesis; (b) repression of maternal protein synthesis; (c) repression of both maternal and paternal protein synthesis; and (d) caste specificity of differential parental protein synthesis in social insects. Although the slow allele at the ACON-1 locus was found only in the China population, our controlled progeny analyses of genotypes at ACON-1 locus did not reveal any allelic repression as is frequently observed in interspecific hybridization (e.g. Hung and Vinson 1977, Hung 1985, Hung and Norden 1987). Both maternal and paternal genes were fully expressed in F_1 and F_2 progeny in our two-way crosses. Therefore, we do not recognize the China population as a separate species. Differences in the percentage of ovipositing females, average fecundity and longevity of females, and number of hosts parasitized were found between the Indian and the Japan "races" of *P. foveolatus* (L. Nong, pers. comm.). However, we believe these biological differences only signify that they are two biotypes. Based on these isozyme analyses, we concluded that there are three biotypes in *P. foveolatus*: I. China biotype with its unique ACON-1 genotype; II. Northern biotype (Japan and Korea) with MDH-1^s allele; and III. Southern biotype (India and Hong Kong) with MDH-1^f allele. The introduced population from Guam apparently belongs to the northern biotype contrary to the expectations based on the historical shipment records.

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A new species of Xus (Order: Family)
injurious to hollies, Ilex spp. (Aquifoliaceae)

John R. Doe and John Smith

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(JS) Entomologist, City Parks, Hartford, Connecticut 06540.

Abstract.- Xus albus, a new species of ... described, illustrated,
and compared with ...

Key Words. Distribution, ornamental shrub, damage, leaf roller

Figure Legends

Figs. 1-4. Xus albus. 1, Habitus. 2, Male genitalia (lateral view)
3, Larva. 4, Pupa.

Fig. 5. Damage to holly leaves.

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(Ilex spp.). Proc. Entomol. Soc. Va. 38: 54-68

(The above citations are fictitious.)

Figs. 1–4. Sample pages for submitted manuscripts. 1, Title page. The mailing address and phone number of the person(s) to whom the page proofs will be sent should be typed in the upper left-hand corner. A proof can be sent to each author of a two- or multi-authored paper if they desire. Affiliation and full address are typed as a paragraph below the author name(s). Spell out the state name. 2, Abstract page. Note that "Abstract" begins the paragraph. On same page, follow abstract with 3–5 key words. 3, Figure legend page. Note punctuation. Start a new paragraph for legends describing each plate. 4, Literature Cited page. Note punctuation and spacing. Authors with access to *Serial Sources for the Biosis Data Base* that is provided with *Biological Abstracts* are expected to use its journal title abbreviations.

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PROC. ENTOMOL. SOC. WASH.
92(1), 1990, pp. 169–170

Book Review

Combating Resistance to Xenobiotics: Biological and Chemical Approaches. M. G. Ford, D. W. Holloman, B. P. S. Khambay and R. M. Sawicki. Ellis Horwood Series in Biomedicine, Ellis Horwood Publishers, 320 pp.

The book is essentially the published outcome of a conference held by the Society of Chemical Industry at Southhampton University in 1986. The purpose of the conference was to discuss the contribution fundamental studies can make to the understanding of pesticide resistance and review how knowledge was being utilized to overcome the problem. The editors have brought together a broad selection of topics addressing these goals. In addition to entomological applications, the book encompasses resistance to antibiotics and a variety of pesticides including fungicides, and herbicides in addition to insecticides. In the forward, D. W. Holloman states that experts from several disciplines sought to link themes of their work on resistance to various antibiotics and pesticides. Accordingly the book is intended to take an interdisciplinary approach.

The introductory chapter "Resistance to pesticides and antibiotics: how far is it comprehensible and manageable?" by I. J. Graham-Bryce does indeed take an interdisciplinary tact, but thereafter the subject matter is presented in a more compartmentalized manner. I will focus my comments on the utility of this opus to entomologists. Of 25 chapters, 10 exclusively address insecticides and two cover insecticides within the broader pesticide context.

The parts of the book on resistance to insecticides, mechanisms of resistance, and structure-activity relationships provide some good general background in these subject areas and some thorough specific information on management of selected pests (e.g. *Heliothis armigera, Lucilia cuprina,* and *Haematobia irritans*). For the beginning student the chapter, by R. Sawicki on definition, detection and documentation provides a concise introduction to terms, parameters, and measurement of resistance. An introduction to the decision making processes for management of resistance in insect pests, by T. J. Dennehy, complements the chapter by Sawicki. The author encourages the reader to know thy: system (is the bioassay appropriate to the agricultural system?); chemical (in addition to mortality, does it have sublethal effects? effects on the rest of the ecosystem? etc.); and target organism (distribution, biology, behavior, stress factors). A very brief portion of the chapter is devoted to the decision making process *per se.* It should be construed more as an outline than a protocol in this regard.

Using *Musca domestica* as their model, I. Denholm et al. present an excellent chapter on laboratory simulation of selection for resistance including a short section on computer modeling of selection rates. They emphasize the importance of understanding the various biological and operational parameters acting at the insect-insecticide interface before selection rates can be accurately modeled.

A short introduction on the genetic aspects of selection for resistance is given by C. F. Curtis. Although the chapter provides a good introduction to the use of numerical and computer models in the genetics context, it does not provide the breadth one is led to expect from its title. The value of pesticide rotation for management of resistance is a useful addition to this chapter and broadly covers the genetic implications of this strategy.

The three chapters on specific resistance management strategies for *Heliothis armi-*

gera, Lucilia cuprina, and *Haematobia irritans* are among the best in the book. Although they each address only one species they give the reader an appreciation for the complexity of the problems and the attention to detail that must be exercised in producing a sustainable solution.

In part 5, Mechanisms of Resistance, only two chapters cover resistance in insects. The chapter by A. C. Baillie is a good introduction to how insecticides work, but falls a bit short on why they fail. Five short paragraphs are devoted to resistance and one to overcoming it. Conversely, the chapter by A. L. Devonshire on biochemical studies of organophosphorus and carbamate resistance in houseflies and aphids provides a detailed account of research conducted on this subject at the Rothamsted Experimental Station. Although not a review of all the mechanisms responsible for resistance in the two test insects to these two classes of insecticides, it does acquaint the reader with an in depth appreciation for two of the mechanisms (e.g. insensitive acetylcholinesterase and insecticide detoxifying esterase) and their measurement.

In the remaining part of the book, structure-activity relationships, only one of the three chapters covers insecticides. In a concise chapter on selectivity and resistance to non-ester pyrethroids and N-alkylamides in houseflies, A. W. Farnham et al. give the reader an understanding of structural effects on insecticidal activity in this increasingly important group of insecticides.

One can truly say this book has something for everyone that may be concerned with resistance to one substance or another. It may have, however, provided excessive material for the IPM specialist concerned only with combating resistance in insects. On the other hand the beginning toxicology student would benefit from the information provided in the non-insecticide portions of the book as well as those dealing with insecticides. However, the book is fairly limited in the depth required for an introductory toxicology course. It should be supplemented with greater detail in the area of structure and activity, the genetics of resistance, and the mechanisms responsible for it. Examples are for the most part drawn from studies of medically important insects. A more detailed sequel should include more examples of resistance in agricultural insect pests.

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PROC. ENTOMOL. SOC. WASH.
92(1), 1990, pp. 171–172

Book Review

Novel Aspects of Insect-Plant Interactions. Edited by Pedro Barbosa and Deborah K. Letourneau. Wiley-Interscience Publications, John Wiley & Sons; New York, Chichester, Brisbane, Toronto, Singapore. 1988. Price: $59.95.

Sixteen scientists have written nine articles on the subject of allelochemical interactions with nearly all of them from the insect ecology point-of-view. The book is divided into four parts each with an introduction by Letourneau. Letourneau says that ". . . this volume represents the forefront of two rapidly advancing areas of ecology: three-trophic level interactions and . . . chemical ecology" (p. 6). Most of the chapters deal with predation and herbivory.

Part I, Conceptual Framework of Three-Trophic-Level Interactions, contains two chapters which discuss plants, insects and allelochemicals. Chapter one is by D. Whitman and is on allelochemical interactions among the three-trophic levels. This chapter categorizes and gives examples of different types of interactions. The second chapter, by D. Nordlund et al., is on allelochemicals and selection behavior of entomophagous insects.

Part II, Microorganisms as Mediators of Intertrophic and Intratrophic Interactions, contains two chapters on the complex involvement of microbes in the interactions between macroscopic organisms. Coevolution of microbes and the insects and microbes and the plants is discussed by M. Berenbaum. M. Dicke tackles the problem of microbial allelochemicals that affect predator behavior.

Part III, Theory and Mechanisms: Plant Effects via Allelochemicals on the Third Trophic Level, discusses the effects of allelochemicals on the food chain. H. Williams et al. cover the topic of parasitoids in the three-level system, emphasizing cotton. Barbosa, in the second paper, proposes the hypothesis for parasitoids, that generalists will suffer greater losses than will specialists from exposure to plant-derived toxins in their hosts.

Part IV, Key Roles of Plant Allelochemicals in Survival Strategies of Herbivores, covers two topics. The first two chapters discuss the ecology of unpalatable prey. J. Pasteels et al. discuss plant-derived defenses in chrysomelid beetles and M. Bowers discusses plant allelochemistry from the standpoint of mimicry. Finally, the last chapter, which was written by L. Brattsten, brings into the discussion the somewhat unrelated topic of man's interference, insecticide resistance.

Most of the articles are up-to-date reviews and they all appear to have excellent reference sections that will be of use to anyone trying to gain some insight into the literature. I think all but the very well informed allelochemical investigator could learn quite a lot reading the volume. Most of the chapters have an introduction that defines terms and they all end with a short discussion on the future. However, I had two problems with this volume, first as a botanist and a systematist I had difficulty with the terminology, much of which was new to me. I found that different authors meant different things although they used the same terms. This is to be expected but because there is no glossary and only a very short subject index I had to search back and forth through the text for definitions. Also, there is no citation index so if one is trying to find if or where a certain reference is cited then one has to look in the reference section of every chapter and then search through that chapter until the location(s) is found. For instance, I wanted to know if Q. Wheeler's fungi-beetle interaction research had

been cited in the text and if so in what context.

The second, and more serious, problem I encountered is that as a systematist I kept asking questions about whether or not these various chemicals were historical, inherited from an ancestral taxon and thereby plesiomorphic, or autapomorphic and therefore candidates for consideration as possible adaptive scenerios. This information was not available and I was left feeling disappointed because it seemed that although much work had been done, basic phylogenetics had been ignored. Ultimately the ones who suffer are those of us who wish to know, not just the facts about the current ecological relationships but also something about the evolution of the organisms involved.

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PROC. ENTOMOL. SOC. WASH.
92(1), 1990, p. 172

Book Review

Cyanide Compounds in Biology. Edited by David Evered and Sara Harnett. John Wiley and Sons Ltd., Chichester, U.K. 1988, IX + 261 pp., $54.95.

This volume covers all of the 15 papers presented at Ciba Foundation Symposium 140 held in Canterbury, England in 1988. Each of the presentations is given *in toto* together with the verbatim discussions following the presentations. All presentations and discussions are in English. Included in the volume are an introduction, three presentations covering the microbial metabolism of HCN and organic cyanide compounds, three presentations on cyanogenesis in higher plants, one presentation on cyanogenesis in insects, one on cyanogenesis in plant-animal interactions, one on methods for determining cyanide and cyanogenic compounds in biological systems, one on the influence of nutritional and biochemical factors on the biological effects of cyanide, one on the mammalian detoxification of cyanide, one on the mechanism of cyanide intoxication and its antagonism, and, last but not least, two general discussion sessions and the chairman's discussion of all presentations. Each of the chapters includes a list of references given alphabetically by author.

This volume should be of considerable interest to biochemists and botanists. Unfortunately, the only presentation of direct (and considerable) interest to entomologists and insect physiologists is that covering cyanogenesis in insects, given by the renowned German insect biochemist Adolf Nahrstedt. However, this presentation is excellent in that it covers very well the information discovered mainly since 1978 concerning the cyanogenic defensive compounds utilized by various beetles (*Leptocoris isolata*) and several species of Lepidoptera (*Zygaena* spp., *Agraulis vanillae,* two species of *Heliconius,* and *Dryas julia*).

All graphs, line drawings, and other illustrations are of high quality, and I could find no grammatical or factual errors in this comprehensive book.

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PROC. ENTOMOL. SOC. WASH.
92(1), 1990, pp. 173–175

Book Review

The Torre-Bueno Glossary of Entomology, compiled by Stephen W. Nichols. New York Entomological Society, % Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. Library order, $45.00; members of the New York Entomol. Soc., $35.00; non-members, $40.00.

J. B. Smith started it with his 154 page "Explanation of Terms Used in Entomology" in 1906. Then in 1937, J. R. de la Torre-Bueno produced his "A Glossary of Entomology, Smith's 'An Explanation of Terms Used in Entomology,' completely revised and rewritten." This was reprinted in 1950. Now we have what purports to be an amplified version of the Torre-Bueno work. By the title it was given, we may assume that its predecessor was uncritically added to, which does indeed seem to be the case. There is a list of 50 "Editorial Contributors."

The original Torre-Bueno work had 323 pages of glossary, 2.1 times as much as the Smith work. The present work has 823 pages of glossary on pages of the same size and with the same size of type as in the earlier work, meaning that it is slightly more than 2.5 times as large. The old work had appendices of abbreviations, symbols, and 9 plates of figures. These are lacking in the new work and no abbreviations are included in the text. This material will be greatly missed.

Bigger is not necessarily better. Has the subject actually grown to the extent that the Glossary has increased? Let us make a few comparisons.

The old work devoted 5 lines to 'aedeagus,' and one phrase 'aedeagal apodeme,' based on that term. The new work has 43 lines, nearly an entire page, on 'aedeagus' and 24 phrases with 'aedeagus' and 'aedeagal.' In the old work, 'aedoeagus' was cited with 'v. aedeagus.' This is as it should be because 'aedoeagus' is no more than a variant of 'aedeagus,' but in the new work 'aedoeagus' is cited and defined as a separate word with no cross-reference to 'aedeagus.' And, the entries for 'penis' and phrases with 'penis' and 'penial' are even more expansive. These and many other cases indicate to what extent the new work is uncritical. The multiplicity of cited phrases is quite evident throughout the new work, although the meanings of many of them are quite obvious from the meanings of the component terms. The many phrases with 'lobe(s)' on p. 407 for the same reason have little claim to inclusion, and Latin 'lobus (pl. lobi)' should appear merely as an equivalent of 'lobe(s).' Much of such expansion of single term definitions results in little more than confusion.

Although many of the main entries in the new work have been expanded, 'venation' has the same inadequate treatment it had in the old work, viz., "the complete system of veins of a wing." It would have been helpful at this point to mention that there have been many systems of terminology for the veins of the wings of insects of various orders, all of which have been virtually superseded by the Comstock-Needham system, one that is convenient to use and applied to all insect wings. Comstock-Needham is entered in the new work, but many workers, especially in orders where the venation is highly specialized, still cling to more or less older systems, particularly in Hymenoptera. It is here that a few figures would have been especially useful. It would at least have obviated the need for making entries for all 6 of the 'longitudinal veins' of the old Schinerian terminology used in Diptera and show at the same time that there

were that many longitudinal veins. A figure would also do much to explain what are 'recurrent veins' (Hymenoptera, etc.).

Words are included that are not or are only marginally entomological, such as 'epiphyte' (botany), 'acid' (chemistry), and 'mineral' (general), as well as the many names cited together with the etiology of diseases of plants (plant pathology), and animals other than insects (medicine).

A few truly entomological subjects have received rather short shrift. One of them is the technique of collection, examination, and preservation of insects. The following are absent: balsam, Canada balsam, Euparal, Cellosolve, medium (mounting, pl. media), macerate, polyporus, silicone, minuten nadel, polyethylene, McPhail trap, Steiner trap, interception trap, even the lepidopterists' old standbys, light trap and light sheet.

Some terminology, such as that for muscles, is still strictly in Latin and should be printed in italics. Latin for descriptions and other uses in entomology has, however, for at least a century been virtually restricted to nomenclature, the scientific names of organisms. Therefore, citations of adjectival terms such as 'nigrescent, nigrescens, nigricante' and 'ferrugineous, ferruginosus, ferruginous' in both the old and the new Glossaries would better have appeared respectively as 'nigrescent (L. *nigrescens, nigricante*),' and 'ferrugineous, ferruginous (L. *ferrugineus, ferruginosus*).' In other words, distinction should have been made between English words and the Latin words from which they have been derived. The definitions for 'efferent' and 'afferent' in both the old and the new Glossaries are poor; including with their definition something about their derivation in such a manner as 'afferent (L. *ad* + *ferens* 'toward-carrying,' and 'efferens (L. *ex.* + *ferens* 'away-carrying')' in itself furnishes a good definition; it is then easy to understand that the duct from the testes to the sperm pump in Diptera is an afferent duct of the sperm pump, while the duct from the sperm pump to the aedeagus is efferent, as well as that the duct from the testes is an efferent duct of the testes. The entry 'ater, atrous, atrus' would better have been omitted entirely; 'ater' is strictly Latin, 'atrous' is long-dead English (not in Webster III, and in the Oxford dictionary as rare (Nat. Hist.), and 'atrus' is only an erroneous form of 'ater.'

Such words as 'phallosome' and 'phallosoma,' instead of being entered separately as if they were distinct words, would better be treated merely as English (with -e) and Latin (from Greek) (with -a) variants of the same word and therefore having different plural forms.

The following important works do not seem to have been used in the compilation of the new Glossary:

Crampton, G. C. 1947. The external morphology of the Diptera. Guide to the Insects of Connecticut, Pt. VI, Diptera; fasc. 1: 110–165 (incl. 14 Pls. of figs. and 13 pp. of bibliography).

Fernald, H. T. 1939. On type nomenclature. Ann. Entomol. Soc. Amer. 32: 689–702.

Hammen, L. von der. 1980. Glossary of Acarological Terminology. Vol. 1, 179 pp. Dr. W. Junk B.V., The Hague.

Lindroth, C. H. 1957. The principle terms used for male and female genitalia in Coleoptera. Opusc. Entomol. 22: 241–256.

And, finally, a few items of miscellaneous comment:

Although the definitions of 'pollinose' and 'pruinose' are correct, mention should have been made that they are often erroneously used for 'microtrichose' and 'microtomentose.'

'Meskatepisternum' (with extra s) is used instead of mesokatepisternum, although McAlpine used merely katepisternum and anepisternum in the Diptera because the corresponding parts of the prothorax and metathorax are not present in that order.

'Aculcus' as used in the female Tephritidae (Diptera) is not mentioned.

'Vertexal' is cited correctly, but no indication is made that it is sometimes used instead of 'vertical' because bristles, etc., so-called are on the vertex and usually are not vertical in the ordinary sense of the word.

'Tragplatte' is a term used in Hennig's earlier work, but supplanted later by 'hypandrium'; it is not the aedeagal apodeme.

'Calcipala' is an organ found in both sexes of Simuliidae.

Special uses of 'cornu' and 'ramus' in the Coleoptera are not cited, nor are the simple meanings of these Latin words, viz., horn and branch, respectively. The entry 'cornua, pl. cornuae' should have appeared under 'cornu' and the fact that 'cornua' is already plural and that 'cornuae' is an incorrect double plural made evident.

'Gymnopedia' should appear with reference to 'pedium.'

'Mesophoba' should appear with reference to 'phoba.'

The new Glossary will do much to fill the gap left by the seriously out-of-date old work, but it is to be fervently hoped that the computer base on which the new work is stored will in not-too-many years from now afford the possibility of producing a much more critical and accurate new edition of it.

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PROC. ENTOMOL. SOC. WASH.
92(1), 1990, p. 176

Book Review

Cotton Insect Pests and Their Management. By G. A. Matthews, Longman Scientific and Technical, Essex, England, Copublished with John Wiley and Sons, New York. 1989. x + 199 pp. $49.95. Cloth.

Improvement of production agriculture in the developing nations of the world is the major emphasis of many international research organizations as well as Third World governments. The development and implementation of integrated, rather than solely chemical pest management is of major importance in many of those countries. Although research on integrated control is far from complete, many advances in the compatible use of insecticides with other control mechanisms are being made.

This book attempts to provide a concise, up-to-date discussion of tropical cotton insect management. It gives the reader the best information available on chemical control methods and shows how these methods affect other control strategies and crop production practices. Research from Africa is emphasized, but management strategies from all cotton production areas are mentioned where appropriate. The author provides a needed, straightforward view of cotton pest management in areas of subsistence agricultural production.

The text is in English and is well written, with the exception of a few minor grammatical/typographic errors. The contents are presented in a logical sequence using nine chapters, with descriptions of the crop and insect pests given first, followed by control tactics and pest management discussions. Figures and tables are of good quality and provide visual illustrations in needed places. Color plates of insects and damage symptoms are exceptionally clear but unfortunately are not available for all of the insects discussed. Inclusion of the additional plates would have been helpful for diagnosing insect pest problems. The number and types of appendices is especially pleasing. These appendices can be used to determine appropriate insect sampling methods, to convert metric units to English units for calibrating sprayers and mixing chemicals, and to determine insect distributions and economic impacts. The Reference section is comprehensive and contains most of the more important citations relating to cotton insect management.

In general I find this book to be a worthy contribution to the science of insect management in cotton. It is an excellent book particularly for people with little or no formal training in insect pest management. It will become a valuable addition to libraries, especially in developing countries, where integrated pest management is in its infancy. Pest management specialists will rapidly adopt this book and it will provide the basis for development of pest control programs on cotton.

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No. 13.	An Identification Manual for the North American Genera of the Family Braconidae (Hymenoptera), by Paul M. Marsh, Scott R. Shaw, and Robert A. Wharton. 98 pp. 1987	18.00

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of the

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PUBLISHED QUARTERLY

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THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

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A SYNOPSIS OF THE SEED-FEEDING GENUS *BEPHRATELLOIDES* (CHALCIDOIDEA: EURYTOMIDAE)

E. E. Grissell and M. E. Schauff

Systematic Entomology Laboratory, USDA, Agricultural Research Service, PSI, % U.S. National Museum NHB 168, Washington, D. C. 20560.

Abstract.—Species of *Bephratelloides* are phytophagous in seeds of *Annona*. Species included in the genus are: *cubensis* (Ashmead), *paraguayensis* (Crawford), *pomorum* (Fabricius) (n. comb. from *Chalcis*), and ***petiolatus*** Grissell and Schauff (new species); *B. maculicollis* (Cameron) is synonymized under *pomorum*; unrecognized species are *limai* (Bondar) and *melleus* (Westwood) (n. comb. from *Eurytoma*) whose types are lost. Six species previously placed in this genus are removed to other eurytomid genera as follows: *Bephrata consobrina* Girault becomes *Bephratoides consobrinus* (Girault) (n. comb.) (with *Bephratoides longigaster* Subba Rao a new synonym); *Bephrata fulviscapus* Girault and *Bephrata bicolor* Girault are transferred to *Eurytoma* (n. combs.) (*Eurytoma bicolor* (Girault) is renamed *giraulti* Grissell and Schauff to avoid homonomy with *Eurytoma bicolor* Walsh); *Bephrata aristidae* Risbec, *Bephrata decaryi* Risbec, and *Bephrata tananarivensis* Risbec are all transferred to the genus *Tetramesa*. An illustrated key is given to the valid species of *Bephratelloides* and all known host and distribution data are summarized.

Key Words: phytophagous, *Annona*, chalcidoidea, Eurytomidae

Bephratelloides is a genus of Neotropical wasps that are phytophagous in seeds of the genus *Annona* from which they emerge and damage ripening fruit. Species of *Bephratelloides* have been reported from Africa (Burks 1971), but we remove them to other genera as explained below. Several species of *Annona* grow naturally in Africa (Palmer and Pitman 1972), so it is possible that *Bephratelloides* occurs there either naturally or as introductions. There is, however, no current evidence that these wasps occur in Africa.

In the Nearctic, *Annona glabra* L. occurs in the southern tip of Florida. *Bephratelloides cubensis* (Ashmead) was reported from this area in the early 1920's (Bruner and Acuna 1923), where it was reared from exotic annonas. According to Hannah Nadel (pers. comm.) *Annona glabra* serves as a host for *Bephratelloides cubensis* but only around plantings of exotic annonas. We believe, therefore, that *Bephratelloides* occurs in the Nearctic as the result of introductions of exotic annonas. Recently the genus has been introduced into new *Annona*-growing areas in Hawaii (Heu 1988), and it might be expected that as more *Annona* is grown commercially there will be more introductions of *Bephratelloides*.

We undertook this study of *Bephratelloides* because of its great economic importance to *Annona* fruit production, because of the recent movement and introduction of these pest species by man, and because the generic placement and specific identity of almost all of the known species was uncertain. No revision of the genus has been previously undertaken.

The known hosts of the genus include 7

species of *Annona* and a commercial hybrid as follows (common names in parentheses): *Annona cherimola* Miller (cherimoya, custard apple), *A. reticulata* Linnaeus (custard apple, bullock's heart, cherimoya), *A. montana* MacFadden (mountain soursop), *A. muricata* Linnaeus (soursop, guanabana, prickly custard apple), *A. squamosa* Linnaeus (sugar apple, custard apple, sweetsop, anon), *A. squamosa* × *cherimola* (atemoya, a commercial cultivar), *A. bullata* A. Richard (unconfirmed), and *A. glabra* Linnaeus (pond apple, alligator apple).

The following abbreviations are used for institutions in the text: ANSP = Academy of Natural Sciences, Philadelphia; BMNH = British Museum (Natural History), London; USNM = U.S. National Museum of Natural History, Washington, D.C.; MNHN = Museum National D'Histoire Naturelle, Paris; ZM = Zoologisk Museum, Copenhagen; ZMHB = Zoologisches museum, Humboldt Universitat, Berlin.

Bephratelloides Girault

Bephrata: of authors, *nec Bephrata* Cameron, 1884: 109.

Bephratoides Girault, 1913a: 60. Preocc. by *Bephratoides* Brues, 1908: 158. Type species: *Bephrata paraguayensis* Crawford, monotypic and orig. desig.

Bephratelloides Girault, 1913b: 459. New name for *Bephratoides* Girault, 1913a.

Burks (1971) redefined *Bephratelloides* and *Bephrata* based upon the type species of each. *Bephrata* was left with only the type species (*Bephrata ruficollis* Cameron) and a statement was made (Burks 1971: 26) that other species of *Bephrata* should be placed in *Bephratelloides* which contained the "phytophagous eurytomids that develop in the seeds of *Annona*." At the time he could not examine each transferred species to determine if its placement was correct, and the result was the creation of two geographically divergent groups of species: one group of 3 from the Ethiopian Region (Risbec 1951, 1952), and another of 7 from the Neotropical Region (DeSantis 1979, 1980). Where biologies were known, one Ethiopian species caused galls on grass stems, and three neotropical species were phytophagous in seeds of *Annona*. Obviously at least one of the Ethiopian species did not fit the "biological definition" proposed for the genus by Burks (1971).

We examined the 10 species referred to above as well as two additional species in other genera, and our findings considerably alter the composition of the genus. All 3 Ethiopian species as well as 3 neotropical species are transferred to other genera. We synonymize one species, transfer two others into *Bephratelloides*, and describe a new species reared from *Annona* seeds from South America. The type material of two species is lost, and we treat them as unrecognized.

Morphological and biological concepts of *Bephratelloides* are now as Burks defined them in 1971. The genus is confined exclusively to the Neotropical Region (except where moved by man) and is the only eurytomid that feeds on fruits of *Annona*. Morphologically it is separable from the large and poorly defined genus *Eurytoma* only in the configuration of the antenna which appears to have 6 flagellomeres and a solid or 2-segmented club. In *Eurytoma* the antenna has 5 flagellomeres and a 3-segmented club.

Key to Species of *Bephratelloides*

1. Scutellum dorsally depressed in profile, projecting noticeably beyond dorsellum (Fig. 3), apex elongated and excised to some extent (Fig. 12); entire propodeum more or less evenly sculptured with setigerous cells (alveoli) (Fig. 5); (size range from 5.5–9.0 mm, large specimens with darkened area under front wing veins) ..... *pomorum* (Fabricius)

– Scutellum evenly arched in profile, scarcely projecting beyond dorsellum (Fig. 4), apex rounded and not excised (Fig. 11); median propodeum sculptured differently than lateral areas, either without alveoli (Fig. 6), or if present, without setae along midline 2

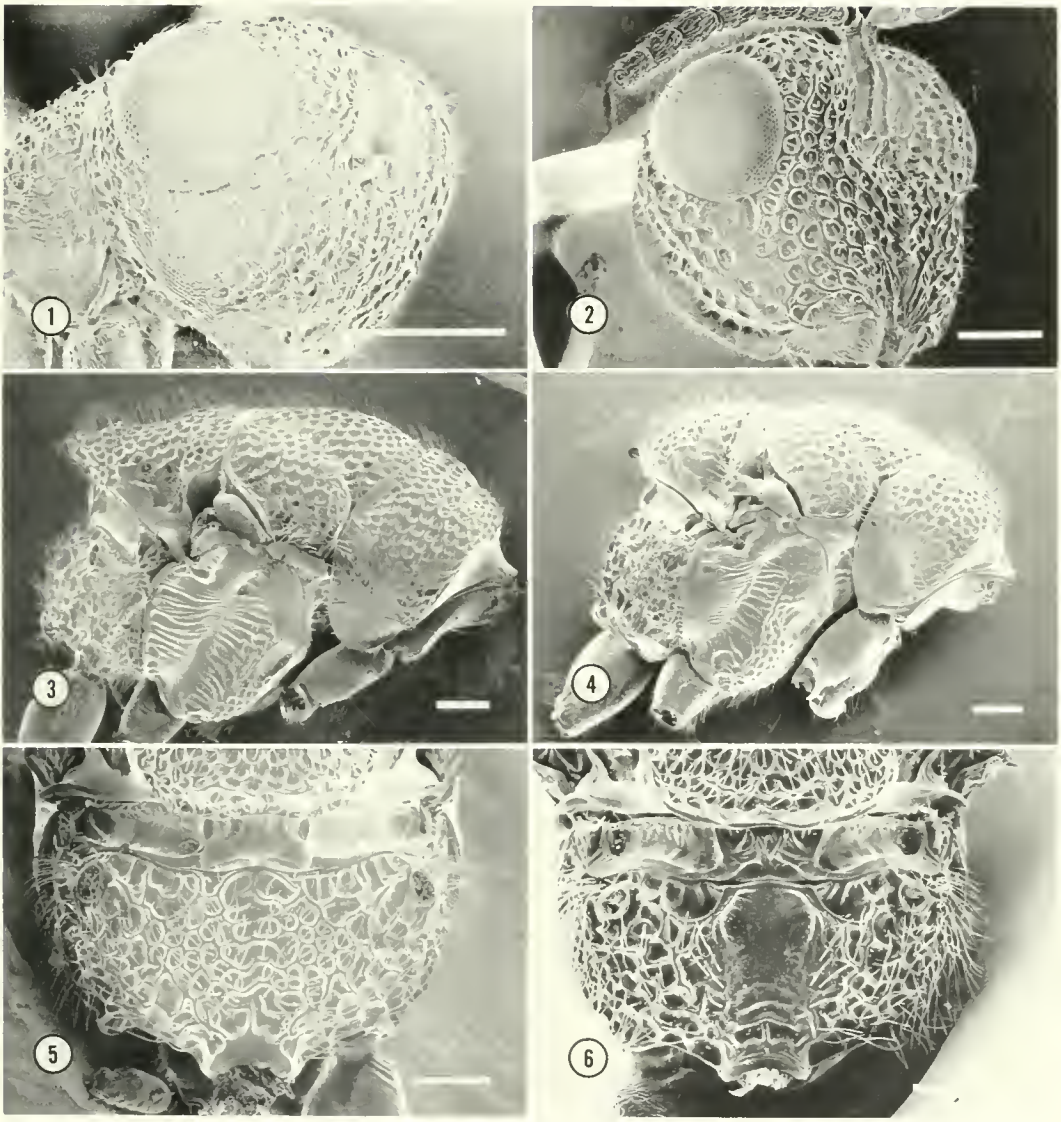

Plate 1. Figs. 1–6. *Bephratelloides* spp. (all ♀), scanning electron micrographs. 1, *petiolatus* head (uncoated). 2, *paraguayensis* head. 3, *pomorum* thorax, lateral view. 4, *cubensis* thorax, lateral view. 5, *pomorum* propodeum. 6, *cubensis* propodeum. Scale line equals 0.25 mm.

2. Median propodeum lacking distinct carinae at least in upper half, nearly smooth (Fig. 6); (size ranges from 4.0–9.5 mm, body color either dark or a mix of orange-yellow with dark markings, large specimens generally with darkened area under wing veins) . . . . *cubensis* (Ashmead)
– Median propodeum with distinct transverse carinae or cells; (size generally under 5 mm, body color all yellowish, occasionally with dark markings on dorsum, wing posteriad to marginal vein either hyaline or with faint stain; Figs. 13, 14) 3
3. Setigerous punctures nearly contiguous under eye (Fig. 2); forewing speculum absent (i.e. area densely setose), cubital vein with setae basally (Fig. 13); male flagellomeres evenly covered with recurved setae (Fig. 9), abdominal petiole 1.5 × as long as wide . *paraguayensis* (Crawford)

Malar space without setigerous punctures (Fig. 1); forewing speculum present (i.e. area bare), cubital vein without setae basally (Fig. 14); male flagellomeres with erect setae arranged more or less in rows (Fig. 10), abdominal petiole 3 × as long as wide .. *petiolatus* Grissell and Schauff

Bephratelloides pomorum (Fabricius), New Combination
(Figs. 3, 5, 8, 12)

Chalcis pomorum Fabricius 1804: 163, ♀. Holotype ♀, ZM [examined].

Bephrata maculicollis Cameron 1913: 121, 1 ♀, "Br. Guiana." Lectotype ♀ (present designation), BMNH, Type Hym 5.78 [examined]. New Synonymy.

Diagnosis.—Female length 5.5 to 9.8 mm. Body color orangish yellow to black, yellowish specimens with at least some black or dark brown spots on the dorsal thorax, forewings usually with conspicuous markings posteriad of veins; scutellum medially depressed, projecting notably beyond dorsellum (Fig. 3), apical margin elongate and slightly to greatly excised (Fig. 12); propodeum (Fig. 5) more or less evenly sculptured with distinct setigerous cells; forewing speculum absent, cubital vein with setae basally. Male flagellomeres cylindrical (Fig. 8), evenly covered with closely spaced bristles which are subequal to segment width or shorter.

This species is easily confused with *cubensis*, which has about the same variation in size and coloration. However, the scutellum of *cubensis* is rounded apically (Fig. 11), is arched in profile and does not project much beyond the dorsellum (Fig. 4), and the median propodeum (Fig. 6) is either smooth (especially anteriorly) or has a few irregular transverse carinae, but no setae.

Discussion.—Z. Boucek (pers. comm.) pointed out to us that *Chalcis pomorum* is a species of *Bephratelloides* and a senior synonym of *maculicollis*. We acknowledge his generosity in allowing us to publish this synonymy as part of our study.

Withing a single rearing, specimens tend to be about the same size, but different rearings result in a range of sizes from about 5 to 10 mm. Smaller specimens may be noticeably different in habitus than large ones. In small specimens the dorsum of the abdomen is nearly horizontal in profile whereas in larger ones the dorsum is arched. Also the apex of the scutellum is somewhat less concave in smaller specimens and the darkened areas of the front wing, under the venation, tend to disappear. Dissection of genitalia revealed no structural differences which might account for the external appearance of the abdomen, and extremes in scutellar development are bridged by intermediate states.

Dominguez Gil (1980) briefly discussed the impact of *cubensis* (cited as *maculicollis*) on *Annona muricata* in the state of Zulia, Venezuela.

Distribution.—We have seen 126 ♀ and 46 ♂ from the following localities: Honduras, Costa Rica, Panama, Trinidad, Tobago, Colombia, Venezuela, Ecuador, Peru, Bolivia, Belize, Surinam, French Guiana, and Brazil.

Hosts.—*Annona cherimola, Annona montana,* and *Annona muricata.*

Types.—The types of *pomorum* and *maculicollis* are both in good condition. The specimen of *maculicollis* in the British Museum is labelled "Lectotype," however this designation has not been published and has no nomenclatural validity. We take the opportunity, therefore, to designate this specimen as lectotype.

Bephratelloides cubensis (Ashmead)
(Figs. 4, 6, 7, 11)

Bephrata cubensis Ashmead, 1894: 321, 3 ♀. Lectotype ♀, ANSP no. 4902 [examined].

Diagnosis.—Female length 4 to 9.5 mm. Body color dark brownish yellow to black, forewings usually with conspicuous mark-

ings posteriad of veins. Scutellum rounded apically (Fig. 11), arched in profile, and not projecting much beyond dorsellum (Fig. 4); propodeum medially (Fig. 6) with a smooth area or with irregular transverse carinae, without setigerous cells; forewing speculum absent, cubital vein with setae basally. Male flagellomeres cylindrical (Fig. 7), setae somewhat aligned in rows separated by distinct bare areas, longer than width of each segment.

This species is most similar to *pomorum* which is about the same size and color. However, *pomorum* has the apical margin of the scutellum excised (Fig. 12), the scutellum depressed in profile and extending notably beyond the dorsellum (Fig. 3), and the median propodeum with setigerous cells (Fig. 5).

Discussion.—As with *B. pomorum, cubensis* has a wide range of variation in size and coloration. Unlike *pomorum*, however, the abdomen does not seem to become horizontal in profile with a decrease in size.

Bephratelloides cubensis and *pomorum* are the two most commonly reared species of the genus. Based upon a study of over 300 specimens, we've noticed a difference in sex ratio between the species. Of 172 *cubensis* specimens only 4 per cent were males whereas of 164 *pomorum* specimens 37 per cent were males. According to Bruner and Acuna (1923) virgin *cubensis* females produce female progeny, and Hannah Nadel (pers. comm.) has told us that males of *cubensis* are "extremely rare" and female progeny are produced from unmated adult females. Thus *cubensis* is a thelytokous species.

Several fairly extensive papers have been published on the biology of *B. cubensis*. Bruner and Acuna (1923) published a review of this species and discussed its biology in Cuba. They included figures of the egg, larva, pupa, and adult as well as photos of larvae within the seeds of *Annona squamosa* and an adult ovipositing into fruit of *Annona reticulata*. Dozier (1932) redescribed the species, showed a photo of damaged fruit (*Annona reticulata*), and cited rearing records in Haiti. Osorio (1937) discussed and figured the immatures, adults, and damage to the fruit. Korytkowski and Ojeda Pena (1966) discuss the biology of the species in Peru on *Annona cherimola* and give numerous figures of morphology including ovipositor, head, mouthparts, wings, and legs.

Distribution.—We have seen 165 ♀ and 7 ♂ from the following localities: United States (Florida, Hawaii), Cuba, Haiti, Puerto Rico, Jamaica, Dominican Republic, Curacao, Mexico, Honduras, Guatemala, Costa Rica, Panama, Venezuela, Colombia. Peru is listed for this species by Korytkowski and Ojeda Pena (1966).

Hosts.—*Annona cherimola, A. muricata, A. reticulata,* and *A. squamosa*. DeSantis (1979) lists *A. bullata* as a host for this species but we have not been able to confirm this record. Nadel (pers. comm.) informs us that *A. glabra, A. montana,* and the commercial cultivar called "atemoya" (*A. squamosa* × *cherimola*) are hosts of *cubensis*.

Types.—Lectotype ♀ (present designation) on point, with data: Cuba. 175,167, Chalcis. *Bephrata cubensis* Ash. Type. Type no. 4902. Deposited in ANSP. The specimen is intact except for the right hindleg, which is missing. Paralectotype ♀ on minuten (USNM), the abdomen was apparently glued separately to a small block of balsa and subsequently lost. Otherwise, the specimen, although covered by dirt, is intact. Ashmead stated that this species was described from 3 ♀. The third specimen is apparently lost as we could not find it in either the USNM or ANSP collections.

Bephratelloides paraguayensis (Crawford)

(Figs. 2, 9, 13)

Bephrata paraguayensis Crawford, 1911: 274. Lectotype ♀, USNM type no. 13801 [examined].

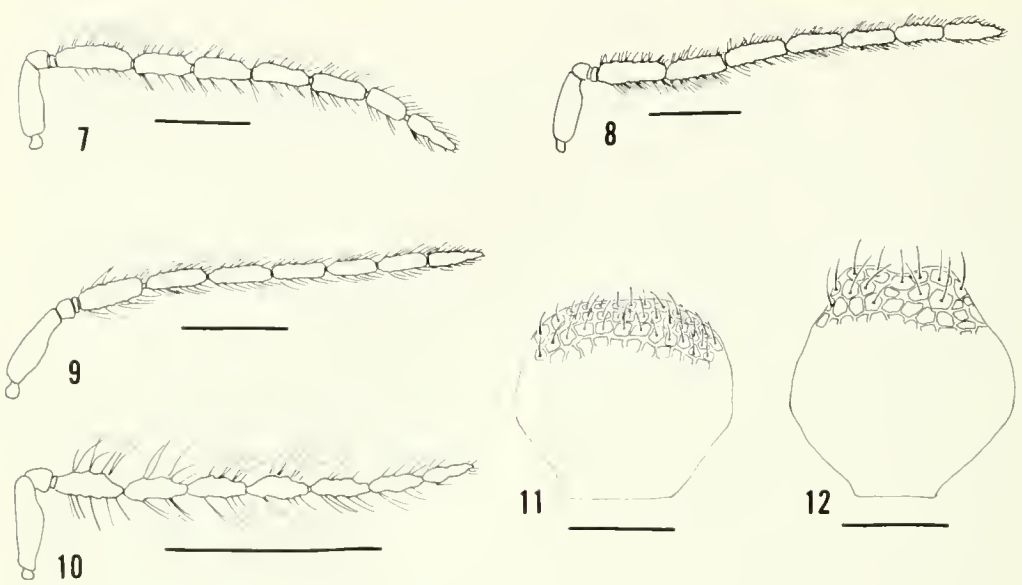

Plate 2. Figs. 7–12. *Bephratelloides* spp. 7, *cubensis* ♂ antenna. 8, *pomorum* ♂ antennae. 9, *paraguayensis* ♂ antenna. 10, *petiolatus* ♂ antenna. 11, *cubensis* ♀ scutellum, dorsal view. 12, *pomorum* ♀ scutellum, dorsal view. Scale line equals 0.5 mm.

Diagnosis.—Female length 5.0 mm. Body color orangish yellow, setigerous punctures under eye nearly contiguous (Fig. 2); scutellum not projecting much beyond the dorsellum, as long as wide, rounded apically; propodeum medially lightly sculptured, without setae along midpoint; forewing faintly darkened posteriad to marginal vein; wing speculum absent, cubital vein with setae basally (Fig. 13). Male flagellomeres cylindrical (Fig. 9), evenly covered with closely spaced, recurved setae.

This species is most similar to *petiolatus* n. sp. and methods to separate them are given under that species.

Distribution.—Paraguay.

Hosts.—*Annona* sp.

Types.—Lectotype female (present designation) on point with data: Paraguay, ex. seeds *Annona*, USNM type no. 13801. Paralectotypes: 3 ♀ and 2 ♂ with same data as lectotype. The antennae from one ♀ paralectotype has been slide mounted. The USNM collection also contains 3 unlabeled specimens of this species that may have been from the same series as the types.

Bephratelloides petiolatus Grissell and Schauff, New Species
(Figs. 1, 10, 14)

Diagnosis.—Length 3.1–3.5 mm. Body color orangish yellow, often with large areas of dark color on the dorsal head and thorax; malar space devoid of punctures (Fig. 1); forewing speculum present (i.e. asetose) and cubital vein basally without setae (Fig. 14); male flagellomeres (Fig. 10) somewhat spindle-shaped, with erect setae 2× as long as width of segment; abdominal petiole about 3× as long as wide.

Males of *petiolatus* may be separated from *paraguayensis* by the ventrally expanded scape (nearly cylindrical in *paraguayensis*, cf. Figs. 9, 10), the pedicellate flagellomeres with erect setae (cylindrical flagellomeres with recurved setae in *paraguayensis*), and the abdominal petiole 3× as long as broad (1.5× as long as broad in *paraguayensis*).

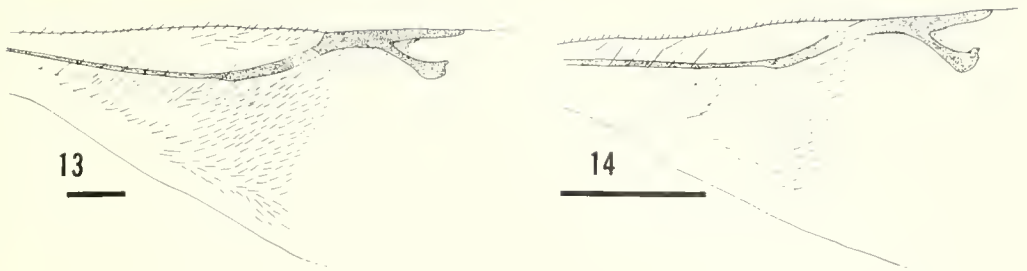

Plate 3. Figs. 13–14. *Bephratelloides* spp., basal forewings. 13, *paraguayensis* ♀. 14, *petiolatus* ♀. Scale line equals 0.5 mm.

Females are more difficult to separate, but *petiolatus* has a nearly smooth area below the eye (*paraguayensis* with scattered setigerous punctures, cf. Figs. 1, 2) and the cubital vein asetose basally (setose in *paraguayensis*, cf. Figs. 13, 14).

Description.—Female length 3.1–3.5 mm. Body color may be completely yellow but with dorsal thorax and abdomen often with large areas of dark brown or black. Head width, at level of eyes, 1.3× height; eye height 1.3× malar space; POL subequal to OOL (8:7); scrobes reaching slightly past midpoint of eye; with large area free of setigerous punctures below eye (Fig. 1); mesoscutum 1.7× length of pronotum (at anterior carina), equal to length of scutellum; pronotum with anterior carina nearly complete, interrupted medially for a length about equal to POL or slightly less; apical margin of scutellum transverse or slightly rounded, not indented; propodeum covered laterally by large irregularly margined punctures which gradually become less pronounced medially, median area covered by irregular transverse carinae, without setae, dorsally about as wide as dorsellum and becoming narrower posteriorly (at posterior margin only about ½ as wide as at anterior margin); petiole 2× as broad as long, dorsally with an upward projecting semicircular median carina; abdomen about equal in length to thorax, about 2× as long (lateral view) as wide (dorsal view), not arched medially; forewing hyaline, without a darkened spot beneath the marginal or stigmal veins, but with a whitish translucent area just below the marginal and adjacent to the stigmal (Fig. 14), speculum present, cubital vein without setae basally.

Male.—Similar to female except for following: generally darker in color with extensive darkened area on the vertex, dorsal thorax, and abdomen (all of the available males were about as dark as the darkest of the females); length 2.3–3.1 mm; antennae as in Fig. 10; abdominal petiole 3× as long as wide; abdomen only about 2× as long as petiole.

Distribution.—Panama.

Host.—Unknown.

Types.—Holotype ♀ on point with data: LaSabanas, Panama City [Panama], J. Zetek Collector. Z-2007. Apr. 9, 1923 (Deposited in USNM). Paratypes: 5 ♀ and 5 ♂ with same data as holotype. All in USNM except 1 ♀ and 1 ♂ in BMNH.

Etymology.—The species epithet refers to the elongate petiole of the males of this species.

Unrecognized Species of *Bephratelloides*

Bephratelloides limai (Bondar)

Prodecatoma limai Bondar, 1928: 83, ♀. Type apparently lost.

Bephrata limai (Bondar); Bondar, 1930: 106. **New Combination.**

Bephratelloides limai (Bondar); DeSantis, 1980: 245. **New Combination.**

Types.—Type material (at least one female) was collected in the state of Bahia, Brazil from seeds of "Anonacea." Attempts to locate this material have failed. According to the original description they should be located at the "Museu Nacional do Rio," but according to its curator, Miguel Monne, they are not there.

Discussion.—Bondar's original description of this species (1928) consists of little more than a general description of body color. He noted that the generally yellow colored body had a black spot or mark between the ocelli and at the foramen on the back of the head. In addition, the antennae were somewhat darker than the rest of the body with the second basal segment (pedicel) almost black and the wings were clear with the stigmal somewhat darkened.

Bondar stated that *limai* was reared from ". . . dementes de varias anonaceas" so there is little doubt that this species belongs in *Bephratelloides*. Its yellow color and 6 mm length would place it near *B. paraguayensis* but without specimens of *limai* we can't be certain of its identity. The problem could be readily resolved by rearing topotypic material from Bahia, Brazil from *Annona* seeds.

Bephratelloides melleus (Westwood), New Combination

Eurytoma mellea Westwood, 1874: 139 (Pl. XXVI, fig. 2), ♀. Type apparently lost.

Type.—This species was apparently described from a single female specimen (based upon a single measurement and figure 2, plate 26). It was reared in Para, Brazil from unknown fruit. The type cannot now be found either at the British Museum (NH) or Oxford Museum (Boucek, O'Toole pers. comm.).

Discussion.—In his discussion of this species, Westwood (1874) compared it to *Chalcis pomorum* (now = *Bephratelloides pomorum*), stating that the two were clearly congeneric. The colored figure of *melleus* also leaves little doubt that it is correctly placed as *Bephratelloides*. There is no doubt in our minds that *melleus* represents either *B. pomorum* or *B. cubensis*, but we cannot make a decision without seeing the type. If it is *pomorum* no nomenclatural problems would arise, but if it is *cubensis* then the name *melleus* would have priority and would replace one of the most commonly collected species of *Bephratelloides*.

Species Transferred from *Bephratelloides*

Bephratoides consobrinus (Girault), New Combination

Bephrata consobrina Girault, 1913a: 60, 1 ♂, San Bernardino, Paraguay. Holotype ♂, ZMHB, examined.

Bephratoides longigaster Subba Rao, 1978: 302–303, 6 ♀, 2 ♂, Nova Teutonia, Brazil. Holotype ♀, paratypes, BMNH; paratype ♀, USNM, examined. New Synonymy.

The male holotype of *Bephrata consobrina* Girault is in nearly perfect condition. Girault reported (1913a) that an "antenna and posterior leg" was mounted on a slide, but we have not seen this material. Based upon the deeply concave occiput, the carinate cheeks, the posteriorly constricted pronotum with tooth-like dorsal sculpturing, the swollen anterior femur with small teeth on the ventral margin, and the placement of the anterior ocellus (located in the scrobal cavity), there is no doubt that *consobrinus* should be placed in *Bephratoides* as defined by Burks (1971). Examination of a paratype female and a male from the type locality (determined by Subba Rao) of *Bephratoides longigaster* Subba Rao (1978) convinces us that it is synonymous with *consobrinus*. Not only is the single diagnostic character the same for both species, (i.e. face longitudinally striate vs. umbilicately punctate in the 4 other known species), but other structural characters such as the carinate scrobal basin, lamellate intercoxal shelf, wing venation, petiolar length and sculpturing, and propodeum are all the same. The distinct coloration is the same as well

(i.e. head yellow with vertex black, and thorax black with all legs including coxae and most of pronotum yellow).

Members of this genus are considered to be parasitic on wood-boring Coleoptera (Burks 1971, 1979).

Eurytoma giraulti Grissell & Schauff, New Name

Bephrata bicolor Girault, 1913a: 59–60, 1 ♀, San Bernardino, Paraguay. Holotype ♀, ZMHB [examined]. [Junior secondary homonym of *Eurytoma bicolor* Walsh, 1870: 298.]

Girault (1913a: 60) suggested that the specimen upon which this species was based might be the female of *Bephrata consobrina* (= *Bephratoides consobrinus*, see above) which was described in the same paper from a male specimen collected at the same locality. The specimens, which were collected four months apart, are remarkably similar in the distinctive color pattern of black and yellow, but other than this are not morphologically very similar. Major differences, generally considered of generic rank, include the following for *bicolor* (contrasting difference for *consobrinus* in parentheses): occiput shallowly concave (deeply concave), ocellus above the scrobal basin (in the basin), anterior femur without teeth on ventral margin (femur with teeth and slightly swollen), pronotum nearly parallel-sided and without enlarged punctures medially which have raised interstices (constricted posteriorly, with enlarged punctures medially which have raised interstices).

The transfer of *bicolor* from *Bephratelloides* is based upon the fact that it has 5 flagellomeres, a longitudinal carina on the outer edge of the forefemur from the base to the apex, and the mesosternum has a carinate shelf below the forecoxae. All of these characters are found in *Eurytoma* but not *Bephratelloides*. Walsh (1870) described *Eurytoma bicolor*, and transfer of *bicolor* Girault (1913a) to *Eurytoma* causes Girault's name to become a junior secondary homonym of Walsh's name. Therefore we must rename Girault's species and we do so in his honor.

Unfortunately the genus *Eurytoma* is not well defined and no natural system of classification exists within it. An examination of this problem is beyond the scope of this paper, but the structural modifications of the thorax found in *bicolor* and some species of *Eurytoma* (i.e. mesosternal shelf and forecoxae grooved for the reception of the head) may indicate a phylogenetically related group of species.

Eurytoma fulviscapus (Girault), New Combination

Bephrata fulviscapus Girault, 1913a: 59, 1 ♀, San Bernardino, Paraguay. Holotype ♀, ZMHB [examined].

The holotype is a typical *Eurytoma* with two outstanding features, namely the first flagellomere and the propodeum. The first flagellomere is tapered from base to apex (ratio of base width : apex width = 9:16), is 4 times longer than basal width (4:17), and is concolorus yellow with the scape and anellus. The propodeal furrow is a parallel-sided, narrow, deep channel which is bounded on either side by a flat, triangular, finely sculptured panel. The ratio of furrow : panel : overall propodeal width is approximately 5:12:65. At the dorsum of the furrow is a pair of pits each of which is flanked on its outer side by a slightly raised carina. Because there is no key to neotropical *Eurytoma*, and because there are a large number of species, it is virtually impossible to place *fulviscapus* without a complete study of the neotropical fauna.

Tetramesa aristidae (Risbec), New Combination

Bephrata aristidae Risbec, 1951: 356–359 (fig. 164), 17 ♀, 15 ♂, M'Bambey, Senegal. Syntypes, MNHN [examined].

We have seen five slide-well mounts (typical of Risbec) containing 23 females and 11 males reared from galls on *Aristida stipoides* (Stipeae: Graminales) from Bambey,

Senegal. Although these specimens are identified as *Bephrata aristidae* and they fit the correct host and locality data as given by Risbec they are not labeled as types of any kind. Selection of lectotype is left to the discretion of the next reviser of *Tetramesa*. This species is placed in *Tetramesa* based upon its lack of a post-genal lamella, the postmarginal and stigmal veins of equal length, the sloping propodeum with an indefinite median furrow, and the association with grass.

Tetramesa decaryi (Risbec), New Combination

Bephrata decaryi Risbec, 1952: 281–283, 1 ♂, Tananarive, Madagascar. Holotype ♂, MNHN [examined].

The male specimen, mounted on a card, is in perfect condition and is easily placed as a *Tetramesa* based upon the lack of a post-genal lamella, the elongate and erectly setose flagellomeres (in male), the absence of a distinct scrobal basin, the yellow markings on the sides of the pronotum, the postmarginal and stigmal veins of equal length, and a sloping propodeum with an indefinite median furrow.

Tetramesa tananarivensis (Risbec), New Combination

Bephrata tananarivensis Risbec, 1952: 284, 2 ♂, Tananarive, Madagascar. Syntypes, MNHN [examined].

The two males of this species are mounted on a single card and are in good condition. They are easily placed as *Tetramesa* for the reasons given under *T. decaryi*. Selection of lectotype is left to the discretion of the next reviser of this genus.

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SHORE-FLY (DIPTERA: EPHYDRIDAE) COMMUNITY STRUCTURE IN SELECTED TERRESTRIAL GRASS HABITATS OF OHIO AND ILLINOIS

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Abstract.—The composition of shore-fly (Diptera: Ephydridae) populations is reported from terrestrial habitats in Illinois for the first time. The consistent collection of ephydrid species in Ohio and Illinois localities substantiates the wider ecological distribution in nearctic terrestrial grass habitats. During spring, the collection of gravid *Leptopsilopa atrimana* (Loew), *Philygria debilis* (Loew), *Hyadina albovenosa* Coquillet, and *Nostima scutellaris* Cresson suggests that these species have encountered physical and biological conditions satisfying minimum reproductive requirements in mowed terrestrial grasslands. Quantitative parameters that include species diversity (H'), evenness (J'), richness (s) and relative abundance (RA), were calculated for several terrestrial grass habitats in Ohio and Illinois. The high inter- and intra-state indices of similarity (I) suggests that these populations are comparable.

Key Words: Diptera, Ephydridae, terrestrial, Sorenson Index

The Ephydridae are one of the most diverse families of cyclorraphous Diptera. Of the 404 nearctic shore-fly species (Deonier 1979), most are semi-aquatic as adults and aquatic as immatures. Dahl's (1959) investigation of Scandinavian Ephydridae represents the first aquatic and marine study dealing with distributional, behavioral, and ecological requirements. Similar investigations have been completed in localized nearctic wetland habitats (Deonier 1965, Scheiring and Foote 1973, Regensburg 1976, Deonier and Regensburg 1978, Steinly 1979, Steinly and Deonier 1980, Zack 1979, 1983, Todd and Foote 1987). These wetland habitats were distinguished by vegetation types and/or substrate constitution in various physiographic regions.

Not all shore-fly habitats occur in wetlands, however. Latreille (1805), Schiner (1864), Rapp (1942), Sturtevant and Wheeler (1954), and Dahl (1959) reported a few distinctly xerophilous ephydrid species. Recently, large numbers of shore flies were collected from dry, palearctic habitats dominated by grasses (Pesková 1978, Bährmann 1978). In a discussion of the life history of *Leptopsilopa atrimana* (Loew), Steinly and Runyan (1979) reported 14 species of Ephydridae collected over a nearctic terrestrial grass lawn. Later, Steinly (1984) compared shore-fly diversity, evenness, richness, and relative abundance values of selected aquatic and terrestrial habitats in Ohio. The quantitative parameters, shore-fly seasonal persistence, and the observed physical, biological, and community differences supported the designation of terrestrial grass as an ephydrid habitat (Steinly 1984).

In this paper, evidence is presented to substantiate the wider ecological distribu-

tion of shore flies in terrestrial habitats. Shore-fly species diversity, evenness, relative abundance, richness, and similarity values in Illinois and Ohio terrestrial grass habitats are compared. Also, quantitative comparisons are made between terrestrial grassland habitats located within each state.

Description of Study Areas

In Oxford, Ohio (Butler County), sampling was initiated over terrestrial grass-dominated lawns and athletic fields on the campus of Miami University. Two grass lawns were also sampled at the Mallot (Steinly and Runyan 1979, Steinly 1984) and Pohl properties 4.0 km and 4.5 km north of Oxford, respectively. Vascular plant species commonly collected from these rural lawns included: *Festuca elatior* Linnaeus, *Cyperus esculentis* Linnaeus, *Digitoria sanguinalis* (Linnaeus) Scopoli, *Setaria faberi* Herrman, *S. lutescens* (Weigel) Hubbard, *Medicago lupulina* Linnaeus, *Muhlenbergia schreberi* J. Gmelin and *Oxalis* sp. Linnaeus (Steinly 1984).

In Illinois, the grass lawns were located in the cities of Urbana, Champaign (Champaign Co.), and Peoria (Peoria Co.). Plant genera commonly encountered included *Festuca* sp. (Meadow fescue), *Digitoria* sp. (crabgrass) and *Cyperus* sp. (sedge). All collecting sites in Illinois and Ohio were well drained, as sufficient slope prohibited surface accumulation of precipitation. Terrestrial grass habitats in Ohio and Illinois were located 0.5 km from the nearest surface water and were not subject to irrigation. All Illinois grass habitats were infrequently mowed and had substantial accumulations of grass clippings in various stages of decomposition. The Miami University lawns were mowed often and dry clippings were rarely observed.

Materials and Methods

Shore flies were collected with a modified aerial sweep net (Regensburg 1977) from 9 March through 15 May 1980 in Ohio. In Illinois, ephydrid specimens were collected from 27 March through 7 May 1981. Habitats were sampled for the same approximate amount of time per visit. Insect samples in collecting bags were immediately killed with ethyl acetate at the site and field-sorted before returning to the laboratory. Pinned and unpinned ephydrid specimens were identified to species. All specimens were examined to ascertain reproductive condition. Voucher specimens will be deposited in the Illinois Natural History Survey Insect Collection.

The percentage relative abundance (R.A.) of each species was calculated for all grassland localities, and the percentage ranges (Scheiring and Foote 1973, Deonier and Regensburg 1978, Steinly and Deonier 1980, Steinly 1984, 1986) were characterized as follows: 1–2% rare (r), 3–8% occasional (occ), 9–14% common (c), 15–25% abundant (a), and 26–100% very abundant (va).

The Shannon-Wiener diversity index (H′) (Scheiring 1974) was calculated because it incorporates species richness (s) and evenness. Diversity was calculated by: $H' = \Sigma\, p_i \log_{10} p_i$ where p_i is n_i/N, n_i is the number of individuals of the i th species of the habitat being considered and N is the total number of individuals per habitat. Several authors (Wilhm and Dorris 1968, Olive and Dambach 1973) have stated that H′ is essentially dimensionless and usually not affected by sample size (N). Sanders (1968), Pielou (1969), Fager (1972), and Simberloff (1972) demonstrated that this index is sensitive to sample size in many instances. Terrestrial habitats of comparable area were sampled for approximately the same amount of time and probable differences in sample size reflect biological differences among the habitats (Scheiring 1974). Evenness (J′) (Scheiring 1974) was calculated by: $J' = H'/\log_{10} s$ where s is the species richness (species number) per habitat.

The community composition of the Ohio mowed grass localities (unpubl. data) were compared by means of the Sorenson index

Table 1. Relative abundance (R.A.) and species number (N) for the Ephydridae in Ohio terrestrial habitats (spring 1980).

Species of Ephydridae	Mallot's			Pohl's			All Localities Except Mallot's			Combined Data		
	N		R.A.	N		R.A.	N		R.A.	N		R.A.
Allotrichoma simplex (Loew)	1	r	(0.1)	—		—	—		—	1	r	(0.01)
Hyadina albovenosa Coquillet	7	r	(0.9)	5	occ	(4.8)	5	occ	(2.2)	12	r	(1.19)
Hyadina binotata (Cresson)	14	r	(1.8)	5	occ	(4.8)	15	occ	(6.6)	29	occ	(2.9)
Hydrellia formosa Loew	27	occ	(3.5)	—		—	1	r	(0.4)	28	occ	(2.8)
Hydrellia griseola (Fallén)	1	r	(0.1)	—		—	1	r	(0.4	2	r	(0.19)
Hydrellia tibialis Cresson	1	r	(0.1)	—		—	—		—	1	r	(0.01)
Leptopsilopa atrimana (Loew)	723	va	(92.5)	90	va	(87.4)	193	va	(85.0)	916	va	(90.78)
Nostima scutellaris Cresson	2	r	(0.2)	—		—	—		—	2	r	(0.19)
Pelina truncatula Loew	—		—	1	r	(1.0)	1	r	(0.4)	1	r	(0.01)
Philygria debilis (Loew)	5	r	(0.06)	1	r	(1.0)	9	occ	(3.9)	14	r	(1.38)
Scatella stagnalis (Fallén)	1	r	(0.01)	—		—	—		—	1	r	(0.01)
Trimerina madizans (Fallén)	—		—	1	r	(1.0)	1	r	(0.4)	1	r	(0.01)
Typopsilopa atra Loew	—		—	—		—	1	r	(0.4)	1	r	(0.01)
Total =	782			103			227			1009		

of similarity (I) with mowed grass habitats in Illinois. Also, grass habitats within each state were compared with the Sorenson index. The similarity index was calculated with the formula I = 2C/A + B, where I is the index of similarity, C is the number of species shared, A is the number of species in habitat A, and B is the number of species in habitat B (Scheiring and Deonier 1979, Steinly 1984). The Sorenson index ranges from 0 when there is no similarity (no species shared) between habitats to 1 when there is complete similarity (all species shared).

Results

At all Illinois localities, the dominant ephydrid species was *Philygria debilis* (Loew) (va) while *Leptopsilopa atrimana* was very abundant only at Champaign (Table 1 and 2). During the spring of 1981 in Illinois, *L. atrimana* number and relative abundance increased slowly while *P. debilis* gradually decreased. *L. atrimana* relative abundance in all Ohio habitats was consistently above 85%. *P. debilis* was rare (r) in the two localities north of Oxford while the species was occasional (occ) in the dryer and more exposed University grass localities.

The examination and dissection of *L. atrimana* (N = 68), *P. debilis* (N = 54), *Nostima scutellaris* Cresson (N = 4) and *Hyadina albovenosa* Coquillet (N = 6) revealed gravid females in Illinois and Ohio grass habitats. Gravid specimens were first discovered in both states during early April.

H', J', and s were lowest for the terrestrial

Table 2. Relative abundance (R.A.) and species number (N) for the Ephydridae (Diptera) in Illinois terrestrial habitats (spring 1981).

Species of Ephydridae	South Farm Urbana			Bradley Park Peoria			West Ells St Champaign			Combined Data		
	N		R.A.	N		R.A.	N		R.A.	N		R.A
Hydrellia formosa	—		—	—		—	1	r	(0.8)	1	r	(0.3)
Hydrellia griseola	—		—	1	r	(0.7)	2	r	(1.7)	3	r	(0.9)
Leptopsilopa atrimana	11	a	(18.9)	12	occ	(8.5)	66	va	(55.0)	89	va	(27.9)
Lytogaster excavata (Sturtevant and Wheeler)	6	c	(10.3)	—		—	2	r	(1.7)	8	occ	(2.5)
Nostima scutellaris	—		—	—		—	2	r	(1.7)	2	r	(0.6)
Philygria debilis	25	va	(43.1)	128	va	(90.8)	46	va	(38.3)	199	va	(62.4)
Scatella stagnalis	14	a	(24.1)	—		—	1	r	(0.8)	15	occ	4.7
Typopsilopa atra	2	occ	(3.4)	—		—	—		—	2	r	(0.6)
Total =	58			141			120			319		

habitat in Peoria (Table 3). In general, however, the Ohio H′, and J′ values were low while richness values were higher than the Illinois habitat values. Comparison of Ohio and Illinois composite H′ and J′ values shows that the Ohio H′ and J′ are approximately two to three times higher than the same parameters in Illinois terrestrial habitats. The relatively high Sorenson Index of similarity (I) (Table 4) suggests the communities within Illinois and Ohio terrestrial habitats were comparable. In Table 4, the high I values generated by comparing habitats within each state suggests these terrestrial habitats have comparable shore-fly communities.

Table 3. Diversity, evenness, and richness values for Ephydridae in terrestrial habitats.

Localities	Diversity (H′)	Evenness (J′)	Richness (s)
South Farm, Urbana	0.60	0.85	5
Bradley Park, Peoria	0.14	0.30	3
West Ells, Champaign	0.43	0.50	7
All Illinois localities composite	0.44	0.49	8
Mallot's 4.0 km north of Oxford	0.17	0.17	10
Pohl's 4.5 km north of Oxford	0.24	0.30	6
All habitats exc. Mallot's	0.28	0.29	9
All Ohio habitats composite	0.20	0.18	13

Discussion

The similarity values generated by comparing grass habitats within each state suggests the intra-state localities have comparable shore-fly populations. Although interstate comparison of the quantitative parameters (H′, J′, and s) suggests the Ohio and Illinois ephydrid communities are distributed and appointed differently within terrestrial grass habitats, the relatively high intra- and interstate similarity indices (I) suggests that these populations are comparable species assemblages. Moreover, the high interstate I value supports the proposed designation of a new terrestrial grass habitat for the Ephydridae (Steinly and Runyan 1979, Steinly 1984).

The interstate variations in locality H′, J′ and s values suggests that the terrestrial hab-

Table 4. Similarity of shore-fly communities in terrestrial grass habitats (Sorenson's Index of Similarity—see text for calculation).

Mallot's—Pohl's, Ohio	0.500
Mallot's—All University habitats, Ohio	0.632
Pohl's—All University habitats, Ohio	0.800
South Farm—Bradley Park, Ill.	0.500
South Farm–Champaign, Ill.	0.667
Bradley Park—Champaign, Ill.	0.600
Ohio—Illinois habitats	0.667

itats in each state have peculiar local physical and biological conditions. Low and high species diversity indices have been associated with habitat physical and biological limiting factors, respectively (Odum 1971). Specifically, species abundance shifts attributed to torrential rainfall, have been recently documented in shore-fly populations (Scheiring and Connell 1988). The high and low relative abundances of *L. atrimana* and *P. debilis*, respectively, in all Ohio localities were not comparable to their relative abundance values in Illinois. In Illinois, the West Ells Street (Champaign Co.) locality had the greatest number of *L. atrimana*. This Illinois locality and the Ohio localities north of Oxford were shaded during the afternoon, sheltered from wind, and had abundant accumulations of grass clippings. In all probability, temperature extremes, exposure to wind, available minimum feeding substrate, and variation in ground-cover density effects species abundance within established shore-fly communities. Additionally, physical constraints may severely limit colonization and/or the utilization of nutrient resources in grass habitats by the Ephydridae. In all probability, grassland habitat colonization by *L. atrimana* and *P. debilis* is dependent on the accumulation and stability of moist decaying vegetation in the microhabitat (Steinly 1984). In vitro, successful *L. atrimana* larval development was dependent on microorganism populations established on the wet surfaces of decaying grass clippings (Steinly and Runyan 1979).

The presence of gravid *L. atrimana*, and *P. debilis* in Ohio and Illinois suggests that minimum reproductive requirements were satisfied in terrestrial grass habitats. Laboratory rearing of *L. atrimana* on wet grass clippings substantiates the probable use of moist microhabitats in habitats traditionally considered terrestrial (Steinly and Runyan 1979, Steinly 1984). Furthermore, a *L. atrimana* larva was field collected from grass clippings by Steinly (1984).

Previously, shore-fly communities in grasslands have been reported from relatively small regions in the Palaearctic (Bährmann 1978, Pesková 1978) and Nearctic (Steinly 1984). The consistent collection of shore flies in terrestrial habitats of Ohio and Illinois and the relative abundance of *P. debilis* and *L. atrimana* demonstrates the wider ecological distribution of ephydrids in nearctic grassland and suggests that shore-fly colonization of terrestrial habitats is not an aberrant phenomenon. Furthermore, ephydrid colonization of terrestrial habitats represents a significant ecological radiation within a trophically diverse family of Diptera.

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SYSTEMATICS OF THE NORTH AMERICAN *CYPHON COLLARIS* SPECIES COMPLEX WITH THE DESCRIPTION OF A NEW SPECIES (COLEOPTERA: SCIRTIDAE)

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Abstract.—North American species of the *Cyphon collaris* complex are revised. Four species are recognized, all from eastern United States, east of the Mississippi River. ***Cyphon drymophilous*** is described as new; *C. dieckmanni* Klausnitzer is synonymized with *C. bicolor* (LeConte), and *C. horioni* Klausnitzer is synonymized with *C. confusus* Brown. Standardized dissection and clearing methods are proposed for studying *Cyphon* genitalia. Salient genitalic characters are illustrated and a key is presented to facilitate identification of adult males.

Key Words: Scirtidae, *Cyphon*

On 19 June 1985, a single specimen of *Cyphon* was collected by the senior author near the eastern boundary of Pine Hollow, a 144 acre State Natural Area in southwestern Wisconsin which is owned and managed by the Nature Conservancy. The specimen, which attracted attention because of its coloration, was collected from a *Rubus* leaf in an upland oak-hickory woodland. Unlike most *Cyphon* which are unicolorous, this specimen had a red-orange prothorax contrasting with an otherwise black body.

Thinking that the color of this specimen might be diagnostic, an attempt was made to determine the species. Upon dissection, what appeared superficially to be *Cyphon collaris* (Guérin-Méneville) turned out to be the male of an undescribed species. In an effort to acquire additional material for examination, subsequent visits to Pine Hollow were made during June and July of 1987. Likewise, loan requests for specimens of *Cyphon* having the *collaris*-like red-orange prothorax were made.

Methods

Measurements.—Using a Wild M5A dissecting microscope with an ocular reticule, specimens were measured for total length (L), measured dorsally along the meson, and humeral width. If the elytra were separated, length was measured along the sutural margin from the anterior mesoscutellar margin to elytral apex. Total length was determined in the following manner: head, pronotum, and elytra were measured separately and recorded. Thus, a value for L was obtained by adding the three measurements (head + pronotum + elytra). This procedure was used due to the considerable variation observed in the distance between the posterior margin of the head and the anterior pronotal margin (i.e. cervical distention) as well as variation in the distention of soft tissue between the prothorax and the elytral bases.

Size range for each species represents the smallest and largest individuals.

Dissection and clearing.—Because of similarity in external appearance it was necessary to dissect all specimens. Since genitalic dissections are generally required for all species determinations of *Cyphon* and standardized techniques have not been established, a detailed account of our procedures is offered: (1) Specimens were boiled in distilled water to rehydrate soft tissues and to remove them from the point or cardmount; (2) the entire abdomen was removed with #5 jeweler's forceps, (3) cleared in hot KOH for 2–4 minutes, (4) rinsed in distilled water, and (5) transferred to a microscope depression slide [with a drop of glycerine]. (6) Genitalia were removed by separating abdominal terga and sterna on one side, laying open the abdomen, and dissecting the aedeagus (male) or prehensor (female).

If genitalic clearing was sufficient at this point, the species determination was made, recorded, and the specimen was transferred to a polyethylene microvial or temporary glycerine storage dish for subsequent examination and comparison with other specimens. If clearing was insufficient, steps 3–5 were repeated.

Specimen preparation for illustration.—The following technique bypasses the need for a heating element to liquefy glycerine jelly and resolves the frustration of having the specimen drift when using pure glycerine. Materials required include: (a) one tube of K-Y Lubricating Jelly *TM—Johnson and Johnson [this is a clear, water soluble semi-liquid jelly]; (b) glycerine; (c) depression slides; and (d) microdissection probes [minuten pins mounted on wooden splints].

Procedural steps.—(1) The glycerine-stored specimen was transferred to a depression slide. [Only the glycerine adhering to the specimen is necessary at this point.] (2) With forceps or the end of a splint, a drop of K-Y gel was placed on the specimen in the depression slide. (3) The specimen was positioned with a minuten (or, very small insect pin) as desired for illustrating. (4) Dehydration [2–3 minutes for the water soluble K-Y gel to lose moisture and specimen to set]. (5) Next, a drop of glycerine was applied over the K-Y (and specimen) to completely cover it [this prevents further loss of moisture]. (6) After waiting 2–3 minutes for K-Y/glycerine interface to stabilize, the specimen was ready for illustration.

Adjusting the specimen to a different view, e.g. dorsal to lateral, often merely requires trial-and-error specimen manipulation. If it is necessary to repeat the procedure, place the specimen with the K-Y gel in warm water. This will dissolve the gel in a matter of minutes. [NOTE: The more time spent during Step 4 before covering with glycerine, the longer gel removal will take.]

Collection acronyms.—For the most part, we have followed the 4-letter entomological collection acronyms proposed by Arnett and Samuelson (1969). Most of these are identified in the acknowledgments but a few exceptions need be noted here. We used the acronym UNHC for the collection at the University of New Hampshire. This slight modification of UNH, which was proposed in Heppner and Lamas (1982), provides uniformity with the 4-letter code recommended by Arnett and Samuelson. Secondly, several of the collections which will receive type material associated with our new species were not sources of specimen loans and are, therefore, not identified in the acknowledgments. These include: the British Museum of Natural History (BMNH), the California Academy of Sciences (CASC), the collections of Daniel K. Young (DYCC) and James B. Stribling (JBSC), and the United States National Museum of Natural History (NMNH).

Taxonomic History and Phylogenetic Considerations

The species long known as "*collaris*" was described by Guérin-Méneville in 1843 un-

der the generic name *Elodes*. The type locality was listed as "Amer. Bor." In 1853, LeConte listed *collaris* from Georgia; he also described *bicolor* from two specimens collected in Georgia. Both were attributed to *Helodes*, following the emendation proposed by Agassiz (1846). Horn (1880) was first to attribute *collaris* to *Cyphon*; he also noted that, " . . . females seem to be very rare." The first recorded bionomical data came from Blatchley (1910). His specimens from Indiana were were collected in early July by sweeping foliage at edges of woods and by beating tamarack. In his contribution to the Coleopterorum Catalogus, Pic (1914) listed *C. bicolor* (LeConte) as a synonym of *Cyphon collaris* (Guérin-Méneville). A similar entry was provided in the catalog of North American Coleoptera (Leng 1920). The holotype male and two male paratypes of *C. confusus* were described from Knowlton, Quebec (Brown 1930). The last two names under consideration were proposed by Klausnitzer (1976). *Cyphon dieckmanni* and *C. horioni* were each described by single males labelled "Alleghany Mt."

As presently understood, the *Cyphon collaris* complex consists of four North American species. It is possible that the two Japanese species, *C. ainu* Nakane and *C. hasegawai* Nakane (Sasagawa 1985), together with these four species constitute a monophyletic group. However, we have not yet examined the Japanese *Cyphon* and we will not consider them further at this time. Like other *Cyphon*, those of the *collaris* complex are extremely similar in external appearance, with distinct and constant variation expressed primarily in the genitalia.

Since we are unable at this point to propose a hypothesis of monophyly for the genus *Cyphon*, we can not propose a phylogeny for the *collaris* complex. However, the species in question do appear to be more closely related to one another than to any species outside the complex. Males of all species have a pair of apically acute, rod-like structures, one on either side of the aedeagus. These have been described collectively as a modified ninth tergum which has become divided and each half rod-shaped (Fig. 14, see also Klausnitzer 1976: fig. 14). [Sexing individuals is readily accomplished since these structures commonly protrude from the end of the abdomen.] The basally bispatulate penis (Figs. 1–10) may be synapomorphic for this group, but such a hypothesis would be premature at this time.

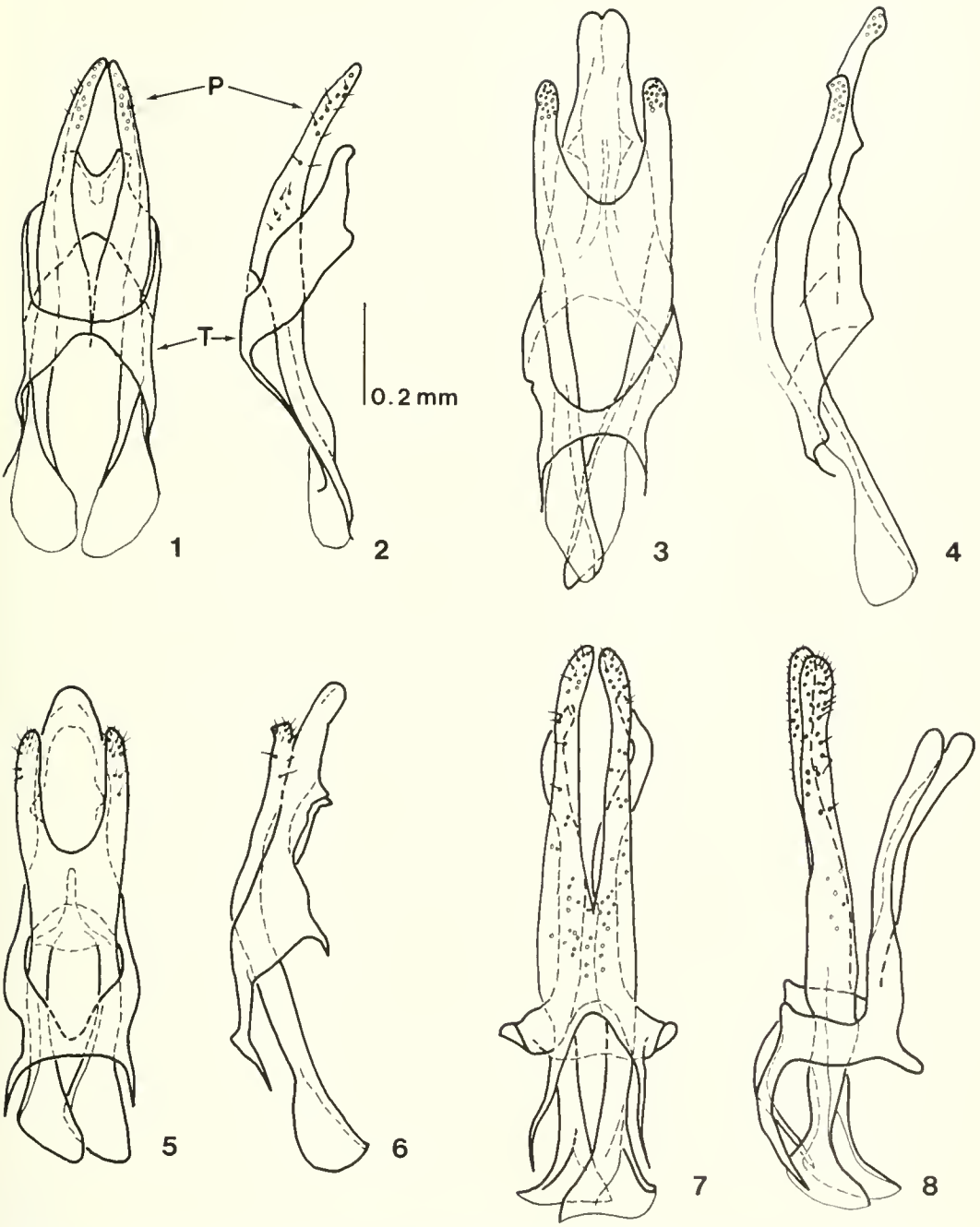
Females of this group appear to be quite rare as Horn perceptively noted over 100 years ago. Of 230 *collaris* group specimens examined in the course of this study, only 36 females were seen. We have been unable to detect any consistent external variation. However, many scirtid females do possess a highly modified and complex sclerotized structure, the prehensor, associated with the internal sack of the reproductive system (e.g. Figs. 11, 13; see also Nyholm 1969 and Klausnitzer 1976). Although the prehensor of females belonging to the *collaris* complex (Fig. 11) is distinct from any examined outside the group, the paucity of females precluded associating the sexes for any species. Thus, while possession of this type of symmetrical, tubular prehensor may be diagnostic for the *collaris* complex, we have not yet been able to use the structure for species-level identification of females.

Systematics

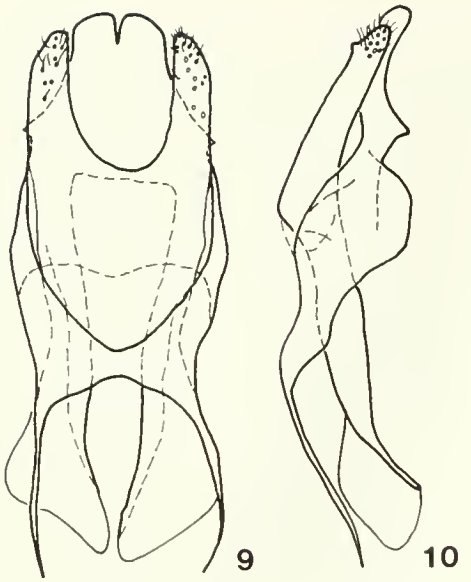
Characters described in the following diagnosis and description are not repeated in the treatment of each species; only diagnostic characters are described therein.

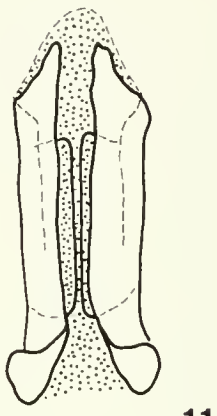
Diagnosis.—This assemblage of species may be distinguished from other *Cyphon* by the moderate size (length 3.9 mm–5.3 mm, humeral width 1.2 mm–1.7 mm), oblong-oval body shape, red-orange to rufotestaceous pronotum and dark brown or black elytra, and genitalic structures. Males possess paired, rod-shaped ninth tergal derivatives, or hemitergites (Fig. 14), and females have a relatively simple prehensor (Fig. 11).

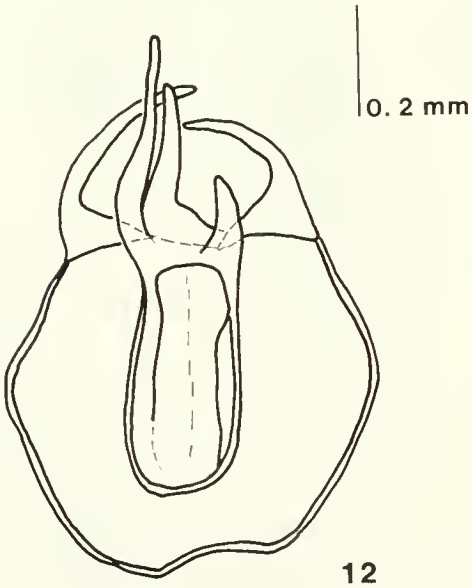
One common species from eastern North

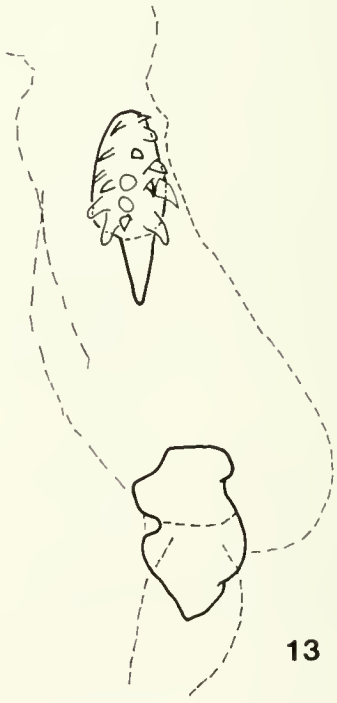


Figs. 1–8. *Cyphon collaris* group, male aedeagus: tegmen (= T) + penis (= P). Figs. 1–2, *C. collaris* (Guérin-Méneville). 1, dorsal view. 2, left lateral view. Figs. 3–6, *C. confusus* Brown. 3 & 5, dorsal view (note variation in apex of tegmen). 4 & 6, left lateral view. Figs. 7–8, *C. bicolor* (LeConte). 7, dorsal view. 8, left lateral view.









Figs. 9–10. *C. drymophilous* n. sp., male aedeagus. 9, dorsal view. 10, left lateral view. Fig. 11, *C. collaris* group female, prehensor (ventral view, caudal end down). Figs. 12–13, *C. ruficollis* (Say). 12, male aedeagus (dorsal view). 13, female prehensor (ventral view, caudal end down).

America which is easily confused with members of the *collaris* complex is *Cyphon ruficollis* LeConte. This species has a similar distribution and coloration, but lacks the rod-shaped ninth abdominal hemitergites and has a very distinctive, asymmetrical aedeagus (Fig. 12) and prehensor (Fig. 13). *Cyphon spinulosus* Klausnitzer (1976) also has a light-colored pronotum. In this species, which is indigenous to California, males lack rod-like ninth abdominal hemitergites; the genitalia are also quite different.

Description.—Head and elytra dark brown or black, pronotum red-orange to rufotestaceous, very rarely brownish. Length 3.9 mm–5.3 mm, humeral width 1.2 mm–1.7 mm.

Head: Usually not visible in dorsal view; antennae with 11 antennomeres; eyes somewhat projecting, interocular distance 3–4× diameter of eye; labrum movable, transverse, basal width approximately 2× mesal length; labial palpi with 3 palpomeres, linear (3rd palpomere arising from apex of 2nd); maxillary palpi with 4 palpomeres, apical palpomere conical; broadly concave ventrally.

Thorax: Pronotal lateral carinae complete, smooth; punctures irregular, separated by more than diameter of a single puncture, each puncture bearing a semi-erect seta; elytra instriate, punctate, slightly rugose with punctures in depressions, each also bearing a semi-erect seta; epipleura complete to elytral apices; prosternum short, intercoxal process thin and blade-like, contacting anterior margin of mesosternum; pro-, meso-, and metathoracic tibiae externally, longitudinally bicarinate, carinae minutely crenulate; tarsi pentamerous, tarsomere 4 bilobed, ungues simple; mesosternal intercoxal process contacting metasternum; metasternum with discrimen complete, transverse suture small, visible only at discrimen near posterior border of metasternum; metathoracic coxae grooved for reception of non-saltatorial femora.

Abdomen: With five visible sterna, 5th entire (males) or emarginate (females); females with cylindrical prehensor (Fig. 11), sclerotized portions divided into 2 longitudinal halves; aedeagus of males (Figs. 1–10) with penis (= median lobe) proximally and distally paired (H—shaped), basally bispatulate, distal arms usually parallel, occasionally convergent (Figs. 1, 7).

Species Key For Males of the *Cyphon collaris* Complex

1. Abdomen with rod-like ninth hemitergites. . . (males, Fig. 14) 2
1′. Abdomen without tergal rods . . females
2. Tegmen apically divided or notched (Figs. 1, 3, 7, 9) 3
2′. Tegmen apically entire, rounded; with median, ventrolateral spines (Figs. 5, 6) . . . . . *Cyphon confusus* Brown (part)
3. Tegmen with median, ventrolateral spines (Figs. 3–4, 9–10) 4
3′. Tegmen without median, ventrolateral spines (Figs. 1, 2, 7, 8) 5
4. Tegmen much narrower and longer than penis; apical notch shallow (Figs. 3, 4) . . . . . *Cyphon confusus* Brown (part)
4′. Tegmen as broad as and but slightly longer than penis, apical notch deep (Figs. 9–10) . . . . . *Cyphon drymophilous*, sp. nov.
5. Tegmen apically divided with each half truncate, much shorter than penis (Figs. 1, 2) . . . . . *Cyphon collaris* (Guérin-Méneville)
5′. Tegmen divided deeply to base, consisting of a pair of rod-like arms (Figs. 7, 8) . . . . . *Cyphon bicolor* (LeConte)

Species of the *Cyphon collaris* Complex

1. *Cyphon collaris* (Guérin-Méneville) (Figs. 1–2, 11, 14)

Elodes collaris Guerin-Meneville, 1843: 4.
Helodes collaris Guerin-Meneville; LeConte, 1853: 355.
Cyphon collaris (Guerin-Meneville); Horn, 1880: 108; Blatchley, 1910: 696 (fig. 269); Pic, 1914: 31; Leng, 1920: 188.

Diagnosis.—Males of this species have the apex of the tegmen divergently bifid with each bifurcation truncate (Fig. 1).

Description.—Aedeagus (Figs. 1, 2). Pe-

nis H-shaped with distal arms parallel, sometimes convergent apically, tegmen shorter than penis, apex divergently bifid with each bifurcation truncate.

Remarks.—The width of the truncate bifurcation varies considerably. The specimen illustrated (Figs. 1, 2) is representative of the majority of males examined in this study. Nyholm (1972: 94, fig. 5F) illustrated a specimen exhibiting wider bifurcations.

Material examined.—*Canada:* Quebec: Knowlton, Que., 29-VI-1930, L. J. Milne, L. J. Milne Collection, 9697 Det. 1934, L. J. Milne (1 male, UNHC). *United States:* Connecticut: Cornwall Ct., 14.VI.1920, K. F. Chamberlain, Cyphon collaris Gu., Chamberlain Collection, Cornell University Insect Collections (1 male, CUIC); Greenwich, Audobon Center, June 12, 1964, David Miller (1 male, AMNH). Delaware: Del. Water Gap., Collection of. Mrs. A. T. Slosson, AC. 26226 (1 male, AMNH). Maine: Dover—Foxcroft, Maine, July 13, 1947, on fir, 9697 (1 male, UNHC); Lincoln, Maine, July 4 (1 male, UNHC); C. A. Frost, Monmouth 26 Je'10 Me., Cyphon collaris Guer, Cyphon collaris Guer Edith W. Mank Collection, Cornell University Insect Collections (4 males, CUIC); Monmouth, VI-26-10 Me., Cyphon collaris Guer., Edith W. Mank Collection, Cornell University Insect Collections (1 male, CUIC); Bar Harbor, Me., 7 Jy 36, Edith W. Mank Collection, Cornell University Insect Collections (1 male, CUIC). Massachusetts: Mass, Cyphon collaris (Guer.), Det. R. Tetrault 1965 (8 males, MSUC); Ashland, Mass., VI-7-25, C. A. Frost, Cyphon collaris Guer., Edith W. Mank Collection, Cornell University Insect Collections (1 male, CUIC); Petersham, Mass., 3-VII-1935, Milne & Green (5 males, UNHC); Boston, Massachusetts, No., Hy. Edwards Collection (1 male, AMNH); Lenox, Mass., July 1, 1891, Bradford Coll. (1 male, AMNH). New Hampshire: A. & G. Acad. Grant, NH, VI-24-75, malaise (1 male, UNHC); Academy Grant, N.H., VI-12-1974, Atkinson and Gilmanton, W. J. Morse, colr (1 male, UNHC); Dover, N.H., VI-15-1934, Basil G. Markos (1 male, UNHC); Dover, N.H., 6-22-1936, B. G. Markos, Cyphon collaris (Guer.), Det. R. Tetrault 1965 (1 male, UNHC); Durham NH, 2460, W&F, Wickham det. 4015 Hensh list (1 male); Lee, N.H., VI-19-'26, P. Lowry, collr., Cyphon collaris (Guer.), Det. R. Tetrault 1965 (1 male, UNHC); S. Albert Shaw, Hampton, N.H., VI-6-1903 (1 male); USA: NH: Coos Co., Norton Pool, 3 mi. NE East Inlet Dam, VI-23-1986, D. S. Chandler, sweep (2 males, UNHC); USA: NH: Coos Co., Norton Pool, 3 mi. NE East Inlet Dam, VI-24-1986, D. S. Chandler, sweep (3 males, UNHC); USA: NH: Rock Co., Newcastle Common, VI-29-1977, TA Glennon, ex: wrack (1 male, UNHC); USA: NH: Straf. Co., 1 mi. SW Durham, V-27/VI-10-1987, D. S. Chandler, FIT (9 males, UNHC); USA: NH: Straf. Co., 1 mi. SW Durham, VI-11/18-1987, D. S. Chandler, FIT (22 males, 1 female, UNHC); USA: NH: Straf. Co., 1 mi. SW Durham, VI-19/VII-1-1987, D. S. Chandler, FIT (4 males, 1 female, UNHC); USA: NH: Straf. Co., 1 mi. SW Durham, VII-2/9-1987, D. S. Chandler, FIT (2 males, UNHC); USA: NH: Straf. Co., Durham, VI-18-'87, W. J. Morse (1 male, UNHC); New Jersey: Anglesea, NJ, H. W. Wenzel, Collection, Cyphon Collaris (Guer.), Det. R. Tetrault 1965 (6 males, OSUC); Chatsworth, N.J., June 15, 1923, J. C. Bradley Coll., Cornell University Insect Collections (1 male, CUIC); Ramsey, N.J., VI.8.1921 (1 male, AMNH); Bergen Co., N.J. (5 males, AMNH). New York: Slide Mt. N.Y., Ulster Co., 6.15–16.1940, H. Dietrich, Cornell University Insect Collections (3 males, CUIC); N. Rchelle, N.Y., VI-15-30, Cornell University Insect Collections (1 male, CUIC); Artist's Brook, Essex Co., 6.19.36 N.Y., H. Dietrich, Cornell University Insect Collections (8 males, CUIC); Orient LI, Aug. '62 N.Y., Roy Latham, Cornell University Insect Collections (3 males, CUIC); Orient, L.I., April 26–39 Roy Latham, Cornell

University Insect Collections (1 male, CUIC); Orient, L.I., July 23, Roy Latham, Cornell University Insect Collections (1 male, CUIC); Darts, N.Y. VIII, Cornell U., Lot 908, Sub 9, Schaeffer Coll., Cornell University Insect Collections (1 male, CUIC); 6.19.1912, Bellport, L.I., Coll. A. Nicolay, Cornell U., Lot 908, Sub 9, Schaeffer Coll., Cornell University Insect Collections (1 male, CUIC); Greenport, L.I. VI-7-1940, Roy Latham, Cyphon ruficollis, Cornell University Insect Collections (1 male, CUIC); 3—Mile Har., L.I., IX-2-39, Roy Latham, Cyphon collaris Guer., Det. Chamberlain, Cyphon collaris, Cornell University Collections (1 male, CUIC); Moloshu, VI.18 N.Y. (4 males, AMNH). North Carolina: Black Mts., V.25 N.C. (1 male, AMNH); Black Mts., V. 31 N.C. (2 males, AMNH); Cranberry, June 9–19 NC (3 male, OSUC); Cranberry, June 9–19 NC, H. W. Wenzel, Collection, Cyphon collaris (Guer.), Det. R. Tetrault 1965 (5 males, OSUC). Pennsylvania: Penn., No., Hy. Edwards Collection, 4399 (1 male, AMNH); Arendtsville, Pa., V-22-1922, S. W. Frost Coll., Cyphon collaris Guer., det. A. B. Wolcott, Cornell University Insect Collections (1 male, CUIC); Bear Meadows, Centre Co., Pa., 2-VI-1975, D. J. Shetlar (1 male, UWEM); USA: PA: Centre Co., Rothrock St. For., Seeger Nat. Area, 900′, VII-9-1984, DS Chandler, sweep (1 male, UNHC); Mt. Pocono, VII.3.30 Pa, JW Green, A. T. McClay, Collection (55 males, UCDC); Tamarack Bog, Tamarack, Clinton Co., PA, 3-VI-1975, D. J. Shetlar (3 males, UWEM). Tennessee: Mt. LeConte, Gt. Smoky Mts., N. Park Tenn., June 13, 1947, H. Dietrich, Cornell University Insect Collections (1 male, CUIC).

2. *Cyphon bicolor* (LeConte)
(Figs. 7–8)

Helodes bicolor LeConte, 1853: 355. (Holotype male [MCZC]. Label data: [orange disk], H. bicolor, Ga., Lec., Type, 2351, collaris 15.) Abdomen and genitalia dissected, cleared, and stored in polyethylene microvial with glycerine.

Cyphon dieckmanni Klausnitzer, 1976: 445. (Holotype male [Naturhistoriches Museum Wein]. Label data: Allegheny Mt., Spaeth, 1902); not examined. NEW SYNONYM

The aedeagus of LeConte's type of *C. bicolor* agrees with Klausnitzer's illustration of *C. dieckmanni* (1976: 444, fig. 15) except for the complete dorsal tegmen ring illustrated by Klausnitzer. It appears that he illustrated the tegmen in three-quarters view, possibly giving an illusion of the presence of the ring connection.

Diagnosis.—*Cyphon bicolor* males may be easily distinguished by the aedeagus (Figs. 7, 8). Distally, the tegmen consists of paired, rod-like arms which nearly reach the apex of the penis.

Description.—Aedeagus (Figs. 7, 8). Penis H-shaped with distal arms apically convergent, tegmen somewhat shorter than penis, consisting of paired, rod-like arms.

Material examined.—Only two other specimens in addition to LeConte's type were examined.

Georgia.—[the type]. Ohio: Delaware VI—4 Co., O., D. J. & J. N. Knull Collrs., Cyphon collaris (Guer.) Det R. Tetrault 1965 (1 male, OSUC); Franklin Co., VI-2-52, O., D. J. & J. N. Knull Collrs (1 male, OSUC).

3. *Cyphon confusus* Brown
(Figs. 3–6)

Cyphon confusus Brown, 1930: 91. (Holotype male [CNCI]. Label data: Knowlton, Que., 11-VII-1929, L. J. Milne, HOLOTYPE, Cyphon, confusus, Brown, No. 3108).

Cyphon horioni Klausnitzer, 1976: 495. (Holotype male [Naturhistorishes Museum Wein]. Label data: Allegheny Mt., Spaeth, 1902); not examined. NEW SYNONYM

The aedeagus of the holotype of *C. confusus* matches Klausnitzer's illustrations of

C. horioni (1976: 446, figs. 17–18), except for the position of slight dentations associated with the distal arms of the penis. Klausnitzer's illustration (fig. 18) shows the dentations as being lateral; in specimens we have seen, the dentations are dorsal (Fig. 10).

Diagnosis.—Males of this species may be distinguished by the aedeagus (Figs. 3–6). The apex of the tegmen is shallowly notched (Fig. 3) or entire (Fig. 5), and has a pair of ventral, mediolateral spines.

Description.—Aedeagus (Figs. 3–6). Penis H-shaped, distal arms parallel, tegmen shallowly notched or entire distally, longer than penis, with paired, mediolateral spines directed ventrally.

Material examined.—Twenty specimens, in addition to Brown's type, were examined. *Canada:* Ontario: Scotia Jct, Ontario, VII-27-30, Wenzel, H. W. Wenzel Collection, Cyphon collaris (Guer.), Det. R. Tetrault 1965 (1 male, OSUC). Quebec: [the type]. *United States:* Michigan: Chippewa Co., Mich. 6-25-60, R. and K. Driesbach (2 males, MSUC). New Hampshire: Dover, N.H., VII-7-34, B. G. Markos/Cyphon collaris (Guer.), Det. R. Tetrault 1965 (1 male, UNHC); S. A. Shaw, Hampton, N.H., VI-14-1934, (1 male, UNHC); S. A. Shaw, Hampton, N.H., VI-18-1934, Cyphon collaris, 9697, Guer (1 male, UNHC); USA: NH: Rock Co., Odiorne Pt., VI-18/21-1983, DS Chandler, window trap (1 male, UNHC); USA: NH: Rock Co., 1 mi. W Odiorne Pt., VI-25/VII-1-1983 D. S. Chandler, malaise trap (1 male, UNHC); USA: NH: Rock Co., 1 mi. W Odiorne Pt., VI-26/28-1983, DSChandler, malaise trap (1 male, UNHC). New York: Slide Mt., N.Y., Ulster Co., 6.24.1934, H. Dietrich, Cornell University Insect Collections (4 males, CUIC). Ohio: Hocking Co., VI-2 O./J. N. Knull Collr. (2 males, OSUC); Hocking Co., VI-12, O., D. J. & J. N. Knull Collrs. (1 male, OSUC); Hocking Co., V-26-38, O., D. J. & J. N. Knull Collrs., Cyphon collaris (Guer.) Det. Knull '43 (1 male, OSUC). Pennsylvania: Pennsylvania, before Oct. 1897, F. Rauterberg Coll., 13382 (1 male, MCPM); Cowan's Gap St. Pk., Fulton Co., Pa., 29-V-1975, D. J. Shetlar (3 male, UWEM); Oakmont, VI-5-'37, Pa., A. C. Miller, Coll., A. C. Miller Collection (3 males, OSUC).

Distribution.—Label data indicate that this species is distributed primarily in the northeastern U.S.

4. *Cyphon drymophilous*, New Species
(Figs. 9–10, 15)

Type information.—Holotype male (USNM): [Wisconsin]: WISC: Sauk Co., Pine Hollow, T10N, R5E, Sec. 04, 19-VI-1985 Daniel K. Young. Paratopotypes (16 males): 10-VI-1987 Daniel K. Young (2 males); 12-VI-1987 Daniel K. Young (3 males); 16-VI-1987 Daniel K. Young (4 males); 24-VI-1987 Kurt Kaiser (3 males); 6-VII-1987 Daniel K. Young (3 males); 6-VII-1987 Rick Ness (1 male). Paratypes (12 males): Wisconsin: WISC: Sauk Co., Baxter's Hollow, T11N, R6E, Sec. 32, 22-VII-1987 Daniel K. Young (1 male); Wis. Milwaukee Co., Before Oct. 1897, F. Rauterberg Coll., 13382 (2 males); Ohio: Delaware Co., VI-21-50 O., D. J. & J. N. Knull Collrs (1 male); Delaware Co., VI-21, O., D. J. & J. N. Knull Collrs (2 males); Delaware Co., VI-2 O., D. J. & J. N. Knull Collrs., Cyphon collaris Guer. Det Knull '55 (1 male); Delaware Co., VI-2 O., D. J. & J. N. Knull Collrs. (2 males); Delaware Co., VI-17 O., J. N. Knull Collr. (1 male); Greene Co., VI-2, O., D. J. & J. N. Knull, Collrs (1 male, OSUC). Illinois: 4225, June, Chicago, Ill. Blackwelder, Collection of Wm. S. Marshall, Cyphon collaris Guer., 4015 (1 male).

Paratopotypes and paratypes are distributed among the following collections: BMNH, CASC, DYCC, JBSC, MCZC, MCPM, OSUC, UWEM.

Diagnosis.—Males of this species (Fig. 15) may be distinguished from others in the *collaris* complex by the aedeagus (Figs. 9–10). The tegmen is notched at the apex with each

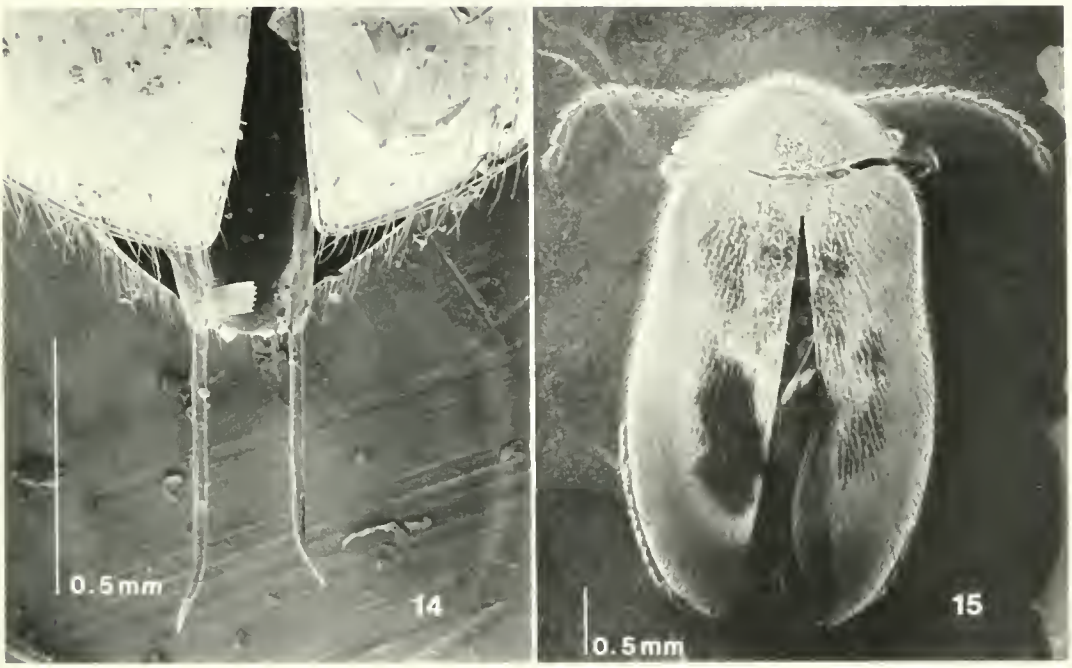


Fig. 14. *C. collaris* (Guerin-Meneville), abdominal apex illustrating rod-like 9th hemitergites. Fig. 15. *C. drymophilous* n. sp., habitus (apparent elytral maculations are artifactual; may represent electron "burning" in this uncoated sample).

side rounded, it has a pair of ventrally projecting, mediolateral spines, and is but slightly longer than the penis.

Description.—Aedeagus (Figs. 9–10). Penis H-shaped, distal arms parallel, tegmen but slightly longer than penis, apex deeply notched with each side rounded and with paired, ventrally directed mediolateral spines.

Remarks.—The species epithet is derived from the Greek "drymo-" meaning a forest or woodland, and "philo," to love. The species name refers to the fact that the type series was collected in a woodland community, unlike the marsh community which is more typically thought of as a *Cyphon* habitat.

Material examined.—As noted above, the type series consists of 29 male specimens.

Distribution.—Records show a distribution from southcentral Wisconsin eastward to central Ohio.

Acknowledgments

We gratefully acknowledge the assistance and cooperation of the following institutions and curators for loans of specimens: American Museum of Natural History (AMNH), Lee Herman; Canadian National Collection (CNCI), Milt Campbell and Laurent LeSage; Cornell University (CUIC), Rick Hoebeke and Jim Liebherr; Michigan State University (MSUC), Roland Fischer and Fred Stehr; Milwaukee County Public Museum (MCPM), Gary Noonan; Museum of Comparative Zoology (MCZC), Jim Carpenter and Charles Vogt; The Ohio State University (OSUC), Charles Triplehorn; the University of California–Davis (UCDC), Robert Schuster; the University of New Hampshire (UNHC), Donald Chandler; and the University of Wisconsin–Madison (UWEM), Jane Harrington and Steve Krauth.

Special thanks are extended to Milt Campbell (CNCI) for loaning us the type of *confusus*, and to Jim Carpenter and Charles Vogt for sending us LeConte's type of *bicolor*. We also acknowledge the Smithsonian Institution, particularly Paul Spangler, for use of facilities at the United States National Museum of Natural History. Thanks are extended to Stanley Carlson and Melissa Curtis for assistance with scanning electron photomicroscopy at the University of Wisconsin–Madison.

This study was supported, in part, by the Lois Almon Small Grants Research Program administered through the Wisconsin Academy of Sciences, Arts and Letters.

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92(2), 1990, pp. 205–207

DISTRIBUTION AND HABITAT OF *DYSCHIRIUS CAMPICOLA* LINDROTH (COLEOPTERA: CARABIDAE) WITH NEW STATE RECORDS FOR OHIO AND ILLINOIS, FIRST RECORDS EAST OF THE MISSISSIPPI RIVER

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Abstract.—*Dyschirius campicola* Lindroth (Coleoptera: Carabidae) is recorded from Ohio and Illinois, first records east of the Mississippi River. The habitat is described and all known locality records are assembled and presented in a range map.

Key Words: habitat, distribution

In 1981, Harry Lee collected a specimen of *Dychirius campicola* Lindroth at a very interesting salt flat habitat in northeastern Ohio. He had learned about this locality through the kindness of James Bissell, Curator of Botany at the Cleveland Museum of Natural History. Lindroth (1961) described this beetle from three widely separated localities in the Great Plains (Manitoba, New Mexico, Texas). At the time of its discovery in Ohio, it was still known only from these three original localities (Erwin et al. 1977). We have subsequently become aware of many more localities for this species based on museum specimens we have seen and on scattered records in recent publications. All of these localities are west of the Mississippi River. Our records from Illinois and Ohio are the first east of the Mississippi. The Ohio specimens represent a considerable eastward extension of the known range of the species. It is our purpose here to discuss briefly the habitat of *D. campicola* and to gather in one place all records in order to give a more complete picture of the known range.

We have seen many specimens of *D. campicola* in the American Museum of Natural History collected by Dr. Lee H. Herman in the course of his studies on the genus *Bledius* (Coleoptera: Staphylinidae). These locality records were recently published (Herman 1986), but only in a table of *Bledius-Dyschirius* associations where they may be overlooked by carabid workers. We thought it prudent to repeat them here and are indebted to Dr. Herman for allowing us to do so. Further records were discovered by Dr. Yves Bousquet and published in a couple of recent papers on *Dyschirius* and other carabids (Bousquet 1987, 1988).

Readers are referred to Herman's work for a more detailed discussion of *Bledius-Dyschirius* associations. We note here only that Herman found *Dyschirius campicola* in association with twelve species of *Bledius*, at least five of which are known to occur in saline habitats. Lindroth (1961, p. 143) mentions the habitat of *D. campicola* as "probably on alkaline places." Our specimens from Painesville, Ohio, were taken on a large salt flat. Dominant plants there, ac-

Fig. 1. Distribution of *Dyschirius campicola* Lindroth. Circles represent specific localities; stars represent state records without further locality.

cording to James Bissell, are *Solidago sempervirens* (Seaside Goldenrod), *Kochia scoparia* (Summer Cyprus), *Suaeda calceoliformis* (Western Sea Blite), *Atriplex patula* (Spearscale) and *Phragmites australis* (Phragmites). The carabid *Bembidion viridicolle* (LaFerte), a member of a group which favors salt and alkaline habitats, was also quite abundant there.

There follows a detailed list of all localities known to us for *Dyschirius campicola*. In parentheses after each locality and date is given the number of specimens (if known) and a collection acronym or a literature reference upon which the record is based. The following acronyms are used: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Carnegie Museum of Natural History (CMNH), Harry J. Lee, Jr., Collection (HJL), and United States National Museum (USNM).

ALBERTA. South Saskatchewan R. x Highway 41, 25–31.VI.1980 (1, Bousquet 1987).

ARIZONA. Cochise Co.: 16.5 mi. N. Douglas, 4700′ (1, Bousquet 1987); Maricopa Co.: Tempe (3, Bousquet 1987).

ARKANSAS. Conway Co.: 7 mi. S. Morrilton (10, Bousquet 1987).

COLORADO. Larimer Co.: 6 mi. N. Loveland, Sept. 10, 1970 (1, AMNH). Pueblo Co.: 20 mi. E. Pueblo, Huerfano R., Sept. 15, 1970 (2, AMNH).

ILLINOIS. Without further locality (1, CMNH).

MANITOBA. Aweme (Lindroth 1961). This is the location of the farm of the entomologist Norman Criddle and is situated about 25 miles southeast of Brandon in the southwest corner of Manitoba near the North Dakota border (Gurney 1977).

NEBRASKA. Garden Co.: Oshkosh near N. Platte R., Sept. 7, 1970 (1, AMNH).

NEW MEXICO. Without further locality (1, CMNH). Bernalillo Co.: Albuquerque (Lindroth 1961).

OHIO. Lake Co.: Painesville, salt flat, u-v light, July 18, 1981 (1, HJL), July 8, 1982 (7, CMNH, HJL).

OKLAHOMA. Alfalfa Co.: 8 mi. N. Jet, Salt Fork of Arkansas River, Great Salt Plains St. Pk., dug from burrows, June 8, 1968 (1, AMNH). Choctaw Co.: Hugo, Red R. (5, AMNH). Kay Co.: 1 mi. E. Ponca City, Arkansas River, burrows in sand, June 17, 1968 (1, AMNH). Logan Co.: Cimarron River, near Coyle (3, Bousquet 1987).

TEXAS. Oldham Co.: 42 mi. S. Dalhart, Canadian River, Sept. 17, 1970 (2, AMNH). Val Verde Co.: Del Rio (Lindroth 1961). Webb Co.: Laredo (USNM).

UTAH. Weber Co.: Roy, 13-VII-1957 (1, CAS).

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THE OCCURRENCE OF *CHAETOSTRICHA* IN NORTH AMERICA, WITH THE DESCRIPTION OF A NEW SPECIES (HYMENOPTERA: TRICHOGRAMMATIDAE)

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Abstract.—The genus *Chaetostricha* is herein reported from North America for the first time. A new species, ***C. thanatophora,*** a parasite of eggs of the mirid *Neurocolpus longirostris* Knight, is described. This species is most similar to two African species, *C. mahensis* (Kieffer) and *C. miridiphaga* Viggiani.

Key Words: Hymenoptera, Trichogrammatidae, *Chaetostricha* taxonomy

Chaetostricha, as currently defined by Doutt and Viggiani (1968), is a moderate-sized genus of 19 species. It has been recorded from all continents except North and South America. *Chaetostricha thanatophora,* a new species described here, is a common parasite of the eggs of *Neurocolpus longirostris* Knight (Miridae) in California. This mirid is a pest of pistachios in the foothill regions of northern and central California wherever orchards are situated adjacent to its primary host plant, California buckeye [*Aesculus californica* (Spach) Nutt.] (Rice et al. 1988). Most of the material of *Chaetostricha thanatophora* was collected by Dr. Richard E. Rice, University of California, during his studies of the biology of *N. longirostris.*

Chaetostricha thanatophora, NEW SPECIES

The following description is primarily based on slide-mounted material. Color pattern and body length were taken from critical point dried specimens killed and preserved in ethanol.

Color: Dark brown with following structures yellow: dorsum and front of head (vertex, frons, lower face), flagellar segments of antenna, midline of pronotum, metanotum, propodeum, base of first segment and apex of last segment of gaster, apex of femora, base and apex of tibiae, tarsi. Color-variable structures as follows: scape, pedicel of antenna entirely brown to almost entirely yellow; scutellum brown or yellow; mesoscutum entirely brown or yellow with two elongate subparallel light to dark brown maculae on anterior ⅔; pronotum with lateral areas entirely brown or extensively marked with yellow; gaster varying from almost entirely brown to brown with two distinct yellow transverse bands on posterior half. Eyes and ocelli red. Color variation is continuous in females. The few males examined have all color-variable structures brown.

Length: 0.9–1.2 mm.

Female.—Body elongate; gaster relatively narrow, gradually tapered to apex (Fig. 1), 1.8× thorax length.

Head: Antenna (Fig. 3) with relative length of scape, pedicel, funicle, club averaging 21.5:15.0:9.0:33.5 (n = 5); pedicel with distinct transverse ridges; two anelli present; funicle subquadrate, two-segmented, F1 very short, closely appressed to F2, F2 varying from as wide as long to 0.8× as wide as long, F2 with a single placoid sensillum; club

three-segmented, ⅓ as wide as long, C1 and C2 subequal in length, length of C2 similar on all surfaces and consequently appearing longer than C1, C1 and C2 slightly longer than wide, C3 longer and much narrower, subconical, slightly longer than C2, ca. ⅖ as wide as long, C1–3 each with two elongate placoid sensilla. Mandible tridentate. Maxillary palp one-segmented. Labial palp one-segmented, short, obsolescent.

Thorax: Mesoscutum, scutellum reticulate, each with two pair of elongate, narrow, spiniform setae. Mesophragma not extending beyond segment 2 of gaster.

Legs relatively elongate, slender; hind femora ca. ¼ as wide as long. Fore tibia spinose on dorsal surface (Fig. 6); size and number of spines variable (3–6, usually three), spine at apical ⅓ of tibia most well developed, the other two at basal ⅔ and apical ⅛, respectively, rarely all spines poorly developed. Relative length of coxa, trochanter, femur, tibia, (tarsi) as follows: fore leg—27:13:37:36:(15:15:15); middle leg—20:15:37:53:(17:14:12); hind leg—35:17:41:60:(17:17:13); fore, middle, hind tibial spurs—5:12:8.

Fore wing (Fig. 4) not noticeably fumate at base, broad, width averaging 0.52 its length (measured from apex of tegula), suboblate apically, widest at apical ⅓; marginal vein elongate, extending 0.46 wing length; stigmal vein constricted at base; relative length of subcostal, premarginal, marginal and stigmal veins 19:11:14:8, resp.; RS_1 well developed; fringe relatively short, longest setae varying from 0.4–0.9 length of stigmal vein. Hind wing (Fig. 5) with three distinct setal tracts on disk; posterior tract with slightly shorter setae than other two, not quite attaining apex of wing; longest fringe setae subequal to greatest wing width (at hamuli).

Gaster: Hypogynium (Fig. 2) relatively short, extending about half abominal length; with a V-shaped sclerotized band apicomedially, each arm of this band with one or two additional narrow, posteriorly projecting thickenings, each bearing a single seta apically; apex of V-band bisetate. Ovipositor extending ventrally along entire gaster but only apical $\frac{1}{10}$ projecting beyond apex (Fig. 1); base of shaft (1st and 2nd gonapophyses) only slightly anterior to gonangulae (ca. $\frac{1}{10}$ of shaft length lies anterior to gonangulae). Hind tibia varying from 0.29–0.35× ovipositor length (ratio not obviously correlated with hind tibial length).

Male.—Similar in most respects to female. Antenna with F2 more elongate, subrectangular in shape, 0.80 as wide as long; C3 shorter, about as long as wide, slightly shorter than C2. Gaster 1.5× length of thorax, blunt apically, last sternite divided. Genitalia structure basically as other *Chaetostricha* but shape unique for genus (cf. Figs. 7 & 8): relatively short, only 0.70× length of hind tibia, only slightly tapered to apex, with unarmed volsellae apically, not overtly bilobate at tip as in congeners.

Variation.—There is considerable color variation in *C. thanatophora.* Large series indicate that it is continuous. Series from Snowline Lodge in Fresno Co. are, on average, lighter with more yellow coloration than those from other locales. Snowline Lodge represents a relatively mesic site. It is the highest elevation in Fresno Co. (1259 m) where *C. thanatophora* was collected, and it is the only collecting area within the Ponderosa Pine belt (R. E. Rice, pers. comm.).

Type information.—Holotype female and allotype from USA, California, Calaveras Co., 5 mi. SE. San Andreas; R. E. Rice, collr.; deposited in the United States National Museum (see Records for information on dates). Nine paratype females from same locality deposited as follows: British Museum (Natural History), 1; Canadian National Collection, Ottawa, 1; University of California, Department of Entomology, Berkeley, 2; University of California, Department of Entomology, Riverside, 4; University of Naples, Institute of Agricultural Entomology, Portici, 1.

All type material is individually mounted in Canada balsam on glass slides.

Etymology.—Greek: "death bearer."

Diagnosis.—The relatively short ovipositor, nonfumate fore wing base, and short funicle separate *Chaetostricha thanatophora* from most congeners. In several species ⅓–½ or more of the ovipositor extends beyond the gaster; in *C. thanatophora* only the apical 1/10 does so. In a few species, such as *C. fumipennis* (Blood), the ovipositor is similarly shortened but the basal half of the fore wing is strongly fumate.

Chaetostricha thanatophora is most similar phenetically to *C. miridiphaga* Viggiani from South Africa (Viggiani 1971) and *C. mahensis* (Kieffer) from the Seychelles (Kieffer 1917). The following comparison with these two species is based on published descriptions, on the badly damaged unique holotype male of *C. mahensis*, on a large series of what almost certainly is *C. mahensis* from Oman, and on two paratypes of *C. miridiphaga*.

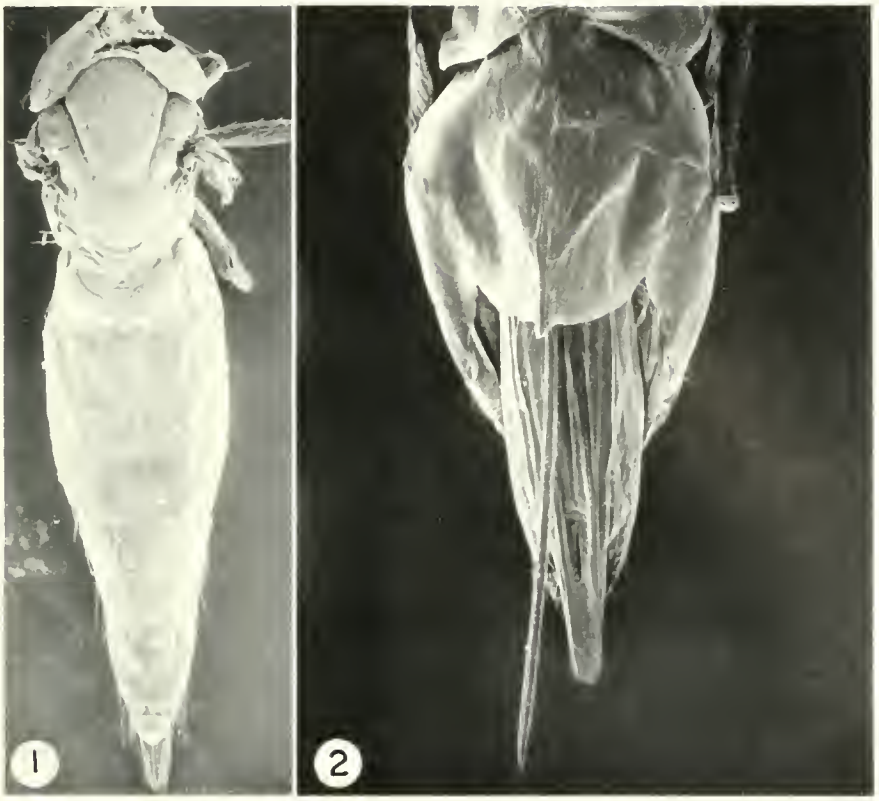
The structure of the antenna, ovipositor and hypogynium, and wing coloration are similar in all three species. However, in *C. thanatophora* the gaster is considerably longer relative to the thorax (1.8× as long) and more distinctly tapered (Fig. 1). In *C. mahensis* and *C. miridiphaga*, the gaster is shorter (ca. 1.4× as long as the thorax) and more ovate in shape (see Viggiani 1971, Fig. 1). Also, the ovipositor is considerably longer in *C. thanatophora*; it runs ventrally along the entire gaster and is over twice the length of the hind tibia. In the two African species the ovipositor occupies only the apical ⅔ of the gaster, and is distinctly less than twice the length of the hind tibia.

The shape of the mesoscutellar setae, the hind wing setal tracts, and the shape of the stigmal vein further distinguish *C. thanatophora* from these African species. In *C. miridiphaga* a distinct posterior setal tract in the hind wing is absent, and the mesoscutellar setae are relatively broad and bladelike, not narrowly spiniform as in *C. thanatophora*. In *C. mahensis* the stigmal is almost perpendicular to the marginal vein, and is strongly constricted basally, resulting in its basal width measuring only ⅓ the greatest width (see Kieffer 1917, fig. 75). In *C. thanatophora*, as in most *Chaetostricha*, the stigmal is less abruptly angled to the marginal vein and less strongly constricted; its basal width is ½ or more its greatest width (Fig. 4).

The most distinctive feature in *C. thanatophora* is the male genital structure. All other known male *Chaetostricha*, including those of *C. miridiphaga* and *C. mahensis*, have the copulatory organ relatively broad basally and tapering markedly to the apex forming a bottle-shaped structure with an apical width less than half the basal width (Fig. 8). The copulatory organ also is longer than the hind tibia in other species. In *C. mahensis*, for example, it is ca. 1.1× as long as the hind tibia, and it is similar in shape and length in *C. miridiphaga*. It is even longer (ca. 1.5× as long as the hind tibia) in most other species. In contrast, the copulatory organ in *C. thanatophora* is of subequal width throughout, not bottle-shaped (Fig. 7), and is much shorter, less than ¾ the length of the hind tibia.

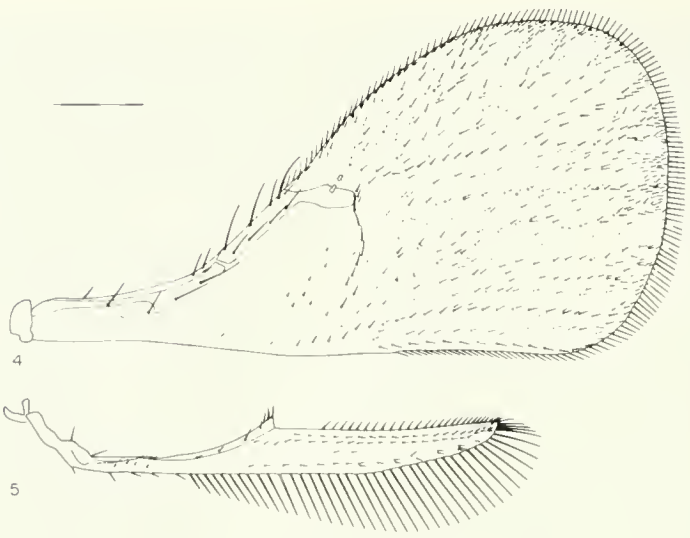
I have seen a few North American *Chaetostricha* in collections in addition to *C. thanatophora*. These are more similar to Old World forms and must be closely compared to that fauna before they are dealt with taxonomically. All are separated from *C. thanatophora* by male genitalia (as above) and ovipositor structure. The ovipositor either is longer in these species (ca. ⅓ of its length extending beyond gaster), the base of the shaft extends considerably anterior to the gonangulae (ca. ¼ the shaft length lies anterior to gonangulae), or the hypogynium is much longer, extending near or beyond the apex of the gaster.

Biology.—*Chaetostricha thanatophora* has been collected from several sites in central and northern California parasitizing eggs of *Neurocolpus longirostris*. Most of the ad-



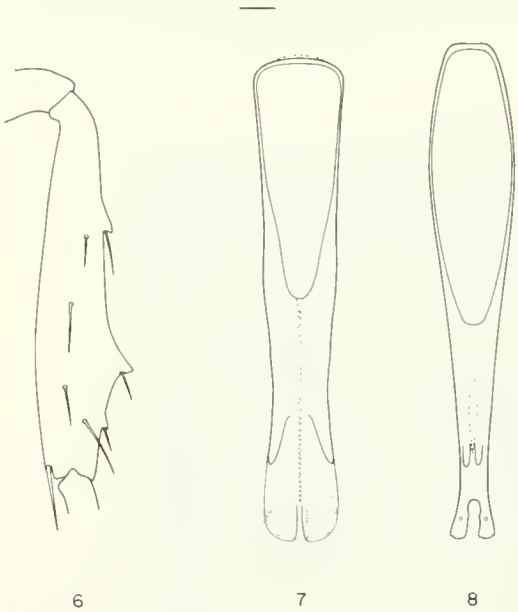
Figs. 1, 2. *Chaetostricha thanatophora*, female. 1, Dorsal view of thorax and gaster (120×). 2, Venter of gaster showing hypogynium and ovipositor (150×).

Fig. 3. *Chaetostricha thanatophora*, female antenna (406×).



Figs. 4, 5. *Chaetostricha thanatophora*. 4, Fore wing. 5, Hind wing. Scale = 0.1 mm.

ditional hosts known for *Chaetostricha* also are Hemiptera: *C. walkeri* (Foerster) from an unspecified Hemiptera (Silvestri 1918); *C. nysiusae* (Risbec) from a lygaeid, *Nysius* sp. (Risbec 1956); *C. miridiphaga* from the mirid, *Lygidolon laevigatum* (Reuter) (Viggiani 1971). The only exception to Hemiptera that I am aware of is a series of an unidentified *Chaetostricha* from Ottawa, Canada, reared from eggs of *Lestes* (Odonata) (unpubl.).



Figs. 6–8. *Chaetostricha* spp. 6, *C. thanatophora*, fore tibia (female). 7, *C. thanatophora*, male genitalia (ventral). 8, *C. mahensis*, male genitalia (ventral). Scale = 0.01 mm.

Males of *C. thanatophora* are extremely rare in collections. Only four of the 332 specimens examined were males. It is not known if this represents the actual sex ratio or if it is attributable to differential mortality prior to adult emergence under laboratory conditions.

Geographic range and records.—UNITED STATES. CALIFORNIA, from the northcentral part of the state in Yolo Co., south to Riverside Co.

The following emerged from *Neurocolpus longirostris* eggs laid in stems of California buckeye, R. E. Rice collr. (The range of dates given below for each series refers to the emergence period of adult wasps in the laboratory; emergence began up to five weeks after field collections of *Aesculus*): *Calaveras Co.:* Carson Hill, 3/V–10/VI, 4 ♀; San Andreas, 5 mi. SE., 19/V–3/VI, 48 ♀, 1 ♂. *Fresno Co.:* Academy, 5 mi. NE. (335 m),

16/III–4/V, 17/IV–12/V, 151 ♀; Piedra (335 m), 8/IV–14/IV, 5 ♀; Snowline Lodge (1259 m) (10 mi. E. Squaw Valley), 19/V–6/VI, 26/V–2/VI, 31/V–13/VI, 33 ♀; Squaw Valley (493 m), 15/IV–7/V, 20 ♀; Watts Valley (491 m) (5 mi. E. Academy), 17/IV–12/V, 9 ♀, 2 ♂; Wonder Valley (283 m) (6 mi. SE. Piedra), 22/IV–4/V, 12 ♀. *Kern Co.:* Stallion Springs (11 mi. SW. Tehachapi), 24/V–3/VI, 19 ♀; Woody, 6 mi. E., 30/V, 2 ♀. *Tuolumne Co.:* Rawhide, 31/V–14/VI, 8 ♀. *Yolo Co.:* Brooks, 31/V–7/VI; Rumsey, 31/V–12/VI, 12 ♀. All of the above locales are in the foothills of the Sacramento (Yolo Co.) and San Joaquin valleys.

Additional records as follows: *Riverside Co.:* Menifee Valley (hills on W. end), 33°39′N., 117°13′W. (550 m), 6–11/X, 1–8/XI, 6–21/IX, 2 ♀, 1 ♂, in yellow pan traps under *Eriogonum gracile* Benth., J. D. Pinto collr. *San Bernardino Co.:* Big Bear City, ca. 1 mi. N., 16/VI, 1 ♀, sweeping willow etc., R. K. Velten collr.

Acknowledgments

Richard E. Rice of the University of California Kearney Agricultural Center sent me numerous collections of *C. thanatophora* and provided information about collecting sites. I also am thankful to John Noyes and Andrew Polaszek of the British Museum (Natural History) for the loan of certain Old World *Chaetostricha* and for permission to remount the type of *C. mahensis,* to Gennaro Viggiani for making paratypes of *C. miridiphaga* available for study, to John Huber for the Oman collection of *C. mahensis,* and to John LaSalle for various favors. Figs. 4–8 were prepared by Linda Bobbitt. SEM photos and study specimens were prepared by Robert Velten.

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THREE NEW IDIOCERINE LEAFHOPPERS (HOMOPTERA: CICADELLIDAE) FROM GUYANA WITH NOTES ON ANT-MUTUALISM AND SUBSOCIALITY

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Abstract.—The species *Rotundicerus minutus* Dietrich, NEW SPECIES, *Rotundicerus rubripictus* Dietrich, NEW SPECIES, and *Chiasmodolon bhagwandorum* Dietrich, NEW GENUS and SPECIES, all from Guyana, are described and illustrated. *Rotundicerus minutus* exhibits egg-guarding behavior and is tended by ants. Three other Guyanese idiocerines, *Chunroides knighti* Maldonado-Capriles, *Hyalocerus* sp., and *Luteobalmus* sp., are also ant-attended, the first occurring in shelters constructed by the ants. The relationships among active, sessile, ant-mutualistic, and subsocial behaviors are discussed with reference to the evolution of the Cicadelloidea and Membracoidea.

Key Words: Ant-leafhopper mutualism, egg-guarding, subsocial behavior, Idiocerinae, Membracoidea, Formicidae

While studying ant-mutualistic and subsocial (*sensu* Wilson 1971) treehoppers (Membracoidea) in the Republic of Guyana, we observed four species of idiocerine leafhoppers in similar situations exhibiting these same behaviors.

Ant-mutualism occurs in several groups of auchenorrhynchous Homoptera, including Fulgoroidea—families Tettigometridae (Lesne 1905), Issidae (Delpino 1875), Delphacidae (Krishna Ayyar 1935; *Peregrinus maidis* Ashmead (as *Pundaluoya simplicia*), and Cixiidae (Myers 1929; *Mnemosyne cubana* Stål)—and Cercopidae (Mann 1915), in which the homopterans occur in the nests of the ants. The only known occurrence of ant-fulgoroid mutualism outside the ants' nest is an observation (Dietrich, unpublished) of *Picumna* sp. issids being tended by formicine ants on the twigs of two unidentified hosts in southern Mexico. Similarly, in some Membracoidea and Cicadelloidea (*sensu* Evans 1947, 1948), ants collect honeydew from the homopterans on the leaves and stems of their host plant. Ant-attendance is common in the Membracoidea and this group is unusual in having numerous subsocial species—i.e. females guard their eggs (Haviland 1925, Hinton 1977, Brown 1976, Bristow 1983, McEvoy 1979, Wood 1984, S.H.M. and C.H.D., unpublished observations).

Reports of ant-leafhopper mutualism are rare in the literature, and egg-guarding behavior has apparently never been documented among the Cicadelloidea. Bergevin (1910) reported ant-attendance of nymphs and adults of the macropsine *Hephathus nanus* (Herrich-Schaffer) in North Africa. Shortly thereafter, Lamborn (1914) gave a detailed account of ant-mutualism for the West African agalliine *Nehela ornata* Dis-

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tant including a description of ant-constructed shelters containing the leafhoppers. Other reports of ant-leafhopper mutualism involve several species of the macropsine genus *Macropsis* (Viraktamath 1980), the ledrine *Petalocephala nigrilinea* Walker (Chatterjee 1934), the iassine *Hishimonus viraktamathi* Knight (Knight 1973), all from India, and members of the Australian cicadelloid family Eurymelidae (Evans 1931). Previous documentation of ant-leafhopper mutualism in the New World is apparently limited to the observations by Beamer and Michener (1950) and Lavigne (1966) of ants tending *Hecalus* (as *Parabolocratus*) spp. (Hecalinae) in Kansas and by Wheeler (1921) of ants tending "jassids" in Guyana (then British Guiana).

We observed four species of idiocerine leafhoppers being tended by ants, at least two of which were apparently also subsocial. One of these was identified as *Chunroides knighti* Maldonado-Capriles. A second species could not be identified based on existing keys and descriptions (see Maldonado-Capriles 1984 for review) and is here described as new and placed in the previously monotypic genus *Rotundicerus* Maldonado-Capriles. The other two ant-attended species, *Hyalocerus* sp. and *Luteobalmus* sp., are also apparently undescribed, but were represented only by females and are not described here.

Two additional idiocerine species were collected at blacklights in Guyana. Both of these also proved to be new, one representing a new genus, and are described below.

Acronyms for collections in which the specimens used in this study are deposited are as follows: NCSU (Insect Collection, North Carolina State University, Raleigh); SHMC (Stuart H. McKamey collection), USNM (United States National Museum of Natural History). In quotations of label data, a virgule (/) separates lines on a label and a semicolon separates information on different labels. Morphological terminology follows that of Maldonado-Capriles (1977a, b, 1984).

Rotundicerus minutus Dietrich, New Species
(Figs. 1–9, 29)

Diagnosis.—This species is much smaller than *Rotundicerus luteus* Maldonado-Capriles and also differs in having characteristic white marks on the forewing membrane, a relatively short ovipositor, and distinctive male genitalia.

Description (males and females).—*Color:* Dull yellow with anterior half of scutellum, thoracic venter, and, in some specimens, femora and ventral part of face dark brown; forewing membrane yellow-hyaline, usually with white marks in inner anteapical cell, along claval suture, and at claval apex, veins and membrane variably infused with dark brown. *Head* (Figs. 1, 2): Face strongly and evenly convex, clypellus constricted medially, approximately 1.33× longer than its apical width, apex slightly narrower than base; lateral margins of genae weakly angulate just ventrad of eyes; upper frontal sutures extending to point directly ventrad of mesal ocellar margins; distance between ocelli about 1.33× distance from ocellus to eye; vertex, in dorsal view, about 3.33× wider than long. *Thorax* (Figs. 2, 3): Visible part of pronotum about 3.4× wider than long in dorsal view; scutellum approximately 1.4× wider than long, in lateral view strongly convex anteriorly; forewing (Fig. 3) with 2 costal, 4 apical, 2 anteapical, and 2 discal cells; inner apical and outer anteapical cells not meeting, separated by a short crossvein; metathoracic femur with small conical projection on upper adlateral surface of base; metathoracic tibial rows I–III with 7–8, 4, and 4–5 stout spines, respectively, row IV with 20+ pale oblanceolate setae; metathoracic tarsomeres I and II with 4–5 and 3–4 cucullate setae, respectively, at apices of plantar surfaces. *Male genitalia* (Figs. 4–9): Pygofer (Fig. 4) with anterior apodemes absent; tergum X with ventral

appendices straight, not L-shaped; subgenital plate (Figs. 4, 5) with apical half, in lateral view, strongly arcuate, dorsal margin with numerous long, fine setae; aedeagus (Figs. 7, 8), in lateral view, with shaft evenly curved anterodorsally, anterior face crenate, in posterior view with shaft widened medially and tapering towards apex; connective (Fig. 6) triangular, lateral ridges forming V-shape and with conical anterodorsal projection; style (Figs. 6, 8, 9) with dorsal setiferous hump, preapical process bulbous and setiferous, apical process acute, arched posteroventrally, in posterior view projecting dorsolaterally. *Female genitalia:* Ovipositor only slightly surpassing apex of pygofer. *Measurements* (mm): body length (to apex of forewing) 2.8–3.1; face length 0.9–1.0, width 1.0–1.1; pronotum width 1.0–1.1; forewing length 2.2–2.4; prothoracic tibia length 0.5–0.6; metathoracic tibia length 1.0–1.1; male plate length 0.5; ovipositor length 1.0.

Material examined.—Holotype male labeled: "GUYANA: Demerara/Co., ca 5 km N of/Kairuni Creek,/G'town-Linden: Hwy, ca km 71, 3/Aug 1987, ca 50 m/C. H. Dietrich; C. H. Dietrich/lot # 87-559; DIETRICH RES./16-88-348e ♂; HOLOTYPE/ Rotundicerus/minutus/Dietrich (USNM, on indefinite loan from NCSU). Other material: 1 male and 6 female paratypes from same locality (NCSU); one additional male and female from Bartica, Mazaruni-Potaro, Guyana (SHMC).

Notes.—This species keys to *Rotundicerus* in Maldonado-Capriles' (1984) key to Neotropical genera. The feature, "ocelli set apart at 2× the distance from ocellus to eye," attributed to this genus therein, is contradicted by Maldonado-Capriles' (1977a) original description and figure of the genus, as well as the condition in *R. minutus*. The semicircular subgenital plate of *R. minutus* resembles that of *Parachunroides* Maldonado-Capriles, but the form of the male genitalia indicates that the new species is more closely related to *R. luteus* Maldonado-Capriles. The trivial name refers to the small size of *R. minutus* relative to its congeners.

Biology.—Based on several sets of observations of ants, reared mymarids, parental females, egg masses, and aggregations of nymphs and adults, we infer the following developmental sequence for *R. minutus*: eggs are inserted almost completely into the stem of woody hosts. The egg mass consists of several close, mostly longitudinal incisions. In some cases, many females oviposit very near each other. The parental female remains atop the egg mass (Fig. 29), unyielding to disturbances. Mymarid parasitoids nonetheless are able to attack some of the eggs. After eclosion, the non-jumping nymphs remain loosely aggregated in the vicinity of the parent. This species was observed on two plant species, being tended by workers of the ant species *Camponotus femoratus* (Fabricius) and *Crematogaster* sp. In one instance, these leafhoppers were associated with a large aggregation of *Tropidaspis* sp. (Membracoidea: Biturritiidae (= Lampropteridae *sensu* Evans 1948)).

Rotundicerus rubripictus Dietrich, New Species
(Figs. 10–19)

Diagnosis.—This species differs from its congeners in the presence of distinct green and red markings on the head and thorax and the distinctive form of the male genitalia.

Description (males and females).—*Color:* Dorsal part of face, vertex and pronotum green with 2 prominent red longitudinal stripes, pronotum with second pair of sublateral red patches; scutellum cream colored, infused with green and with yellowish medial patch and yellowish triangular mark at each anterior corner; forewing smoky hyaline, variably infused with white, veins and membrane marked with dark brown (Fig. 12), clavus with red basal stripe flanked by green stripe that extends to suture, area between claval suture and vein Cu red ba-

sally; remainder of body yellow to light brown. *Head* (Figs. 10, 11): Face strongly convex, about 1.2× wider than long; clypellus inflexed medially, apex slightly produced; genae with lateral margins slightly inflexed, with short, stout, pale seta ventrad of each eye; antennal flagellum with 2 long subbasal trichoid sensilla; distance between ocelli about 2× distance from ocellus to eye; vertex about 2.25× wider than medial length. *Thorax* (Figs. 11, 12): Pronotum about 2.4× wider than medial length; scutellum about 1.4× wider than long, in lateral view appearing more or less flat; forewing (Fig. 12) with apical cell III lacking basal crossvein; metathoracic tibia setal rows I–III with 12–14, 6, and 5–6 spurs, respectively, row IV with numerous pale oblanceolate setae each paired with a short seta 0.25–0.33× as long; metathoracic tarsomeres I and II with 5 and 4 apical cucullate setae, respectively, on plantar surfaces, tarsomere I with dorsoapical pair of setae. *Male genitalia* (Figs. 13–19): Pygofer (Fig. 13) with pair of broad dorsal anterior apodemes, posterior membranous area bounded ventrolaterally by sclerotized ridge with short dorsoapical projection and small oval sclerotized apical plate (Fig. 15), membranous area with numerous short darkly pigmented setae; tergum X (Fig. 13) with distinct ventrolateral emargination and hooked basolateral appendix; plate (Fig. 14) with apex slightly compressed and bearing a few stout setae; aedeagus (Figs. 17, 18) short with apex acute and curved anterodorsally, apical third crenate posteriorly, ventral process in posterior view ovoid; style (Figs. 16, 18, 19) with dorsal setiferous hump, preapical process bearing a few stout setae, apex directed dorsolaterally; connective (Fig. 16) somewhat flattened, with small, acute posterodorsal knob. *Female genitalia:* Ovipositor exceeding apex of pygofer by about 2× ovipositor width. *Measurements* (mm): Body length 3.9–4.1; face length 1.4, width 1.6; pronotum width 1.4–1.5; forewing length 3.3–3.4; prothoracic tibia length 0.8; metathoracic tibia length 1.5, male plate length 0.5; ovipositor length 1.4.

Material examined.—Holotype male labeled: "GUYANA: Mazaruni/Potaro, Isl. ca 35/air km SW Bartica; ca 95 m, 17–18 July/1987, C. H. Dietrich; DIETRICH RES./14-89-15i ♂; HOLOTYPE/Rotundicerus/ rubripictus/ Dietrich" (USNM, on indefinite loan from NCSU). Other material: 3 female paratypes, same data (all NCSU).

Notes.—The presence of a stout seta below the eye of *Rotundicerus rubripictus* suggests that the species might be placed in *Optocerus* Freytag. Nevertheless, the structure of the male genitalia and wing venation, which differ drastically from the type of *Optocerus*, are so similar to those of *R. luteus* Maldonado-Capriles, that the new species' more appropriate placement appears to be in *Rotundicerus*.

The type-series was collected at a blacklight on a forested island in the Mazaruni River near Bartica, Guyana. The trivial name refers to the red patches on the head and thorax.

Chiasmodolon Dietrich, New Genus

Type species: *Chiasmodolon bhagwandorum* Dietrich.

Diagnosis.—These leafhoppers would key out to *Chileanoscopus* Freytag in Maldonado-Capriles' (1984) key to Neotropical genera. However, they lack subapical setae on the hind femora and differ sufficiently in other respects from *Chileanoscopus* and other described Neotropical genera to warrant their placement in a new genus. The following combination of diagnostic characters should distinguish *Chiasmodolon* from other Idiocerinae: coloration not mottled, face flattened and as wide as long, forewings hyaline with veins dark and with 2 anteapical cells, the outer cell not widened apically, male pygofer with pair of mesally directed blade-like projections, aedeagus without crenulations or lateral processes.

Description (males and females).—*Color:* Yellowish, with sparse obscure brown markings; forewings smoky hyaline, veins dark. *Head* (Figs. 20, 21): Face about as wide as long, flattened medially, with 1 or 2 small setae on genal margins just ventrad of each eye; lorae extending to ventral margins of genae; clypellus with margins subparallel, slightly inflexed; antennal flagellum with 2 long subbasal trichoid sensilla. *Thorax* (Figs. 21, 22): Scutellum only slightly convex; forewing with 2 anteapical and 4 apical cells, outer anteapical cell not widened towards apex, outer apical cell with base acute, apical cell II parallel-sided; metathoracic femur without subapical seta; metathoracic tibial row IV with numerous long, pale oblanceolate setae, each paired with a short seta about half as long. *Male genitalia* (Figs. 23–28): Pygofer with pair of acute, mesally projecting crossed processes on dorsum just posterad of base of tergum X, each lateroapical margin produced into an auriculate process; subgenital plate somewhat compressed apically, apex bearing stout setae; aedeagus smooth and narrow, without crenulations or lateral processes, base of shaft with dorsal and ventral processes, apex acuminate; style with prominent preapical process bearing stout setae and a dorsal setiferous hump; connective with dorsal anteriorly acuminate keel. *Female genitalia:* Ovipositor exceeding pygofer by about 2× ventral width of ovipositor.

Chiasmodolon bhagwandorum Dietrich, New Species
(Figs. 20–28)

Description (males and females).—*Color:* As described for genus; clypeus with 7 sublateral brown dashes, brown dash below each ocellus at apex of upper frontal suture, brown spot laterad of each ocellus and a brown patch between ocelli; ocelli bordered with brown; narrow brown medial stripe extending from face between ocelli over vertex to posterior margin of pronotum, pair of wider diagonal stripes extending from just dorsad of ocellus dorsolaterally to posterior margin of vertex; scutellum with 2 anterolateral brown triangles and distinct black mark near midpoint of lateral margin; forewing with distinct black mark near base of corium; first abdominal sternum yellow, remainder brown. *Head* (Figs. 20, 21): Face as wide as long, genae nearly straight, with slight notch just ventrad of mesal margin of eye; vertex about 6× wider than median length. *Thorax:* Pronotum about 2.6× wider than long, scutellum slightly shorter than wide; forewing as described for genus, costal margin infused with yellow-green opaque sclerotization; metathoracic tibia with rows I–III with 22–23, 7–8, and 8–9 stout spurs, respectively, row IV as described for genus, with 3–5 relatively stout subapical setae; metathoracic tarsomeres I and II with 5 and 4 apical cucullate setae, respectively, on plantar surfaces, tarsomere 1 with a dorsoapical pair of setae. *Male genitalia* (Figs. 23–28): Pygofer (Fig. 23) as described for genus, anterior apodemes broad; tergum X not modified; plate (Fig. 24) with 2 or 3 stout apical setae in addition to numerous fine setae on dorsal margin; aedeagus (Figs. 26, 27) in lateral view sinuate, anterior process in posterior view parallel-sided; style (Figs. 25, 27, 28) with preapical process bearing 2 relatively stout setae. *Female genitalia:* As described for genus. *Measurements* (mm): Body length 6.2–6.5; face length 2.3–2.4, width 2.3–2.4; pronotum width 1.9–2.1; forewing length 5.4–5.5; prothoracic tibia length 1.4; metathoracic tibia length 2.4–2.7; male plate length 0.8; ovipositor length 1.3.

Material examined.—Holotype male labeled: "GUYANA: Mazaruni/Potaro, Isl. ca 35/air km SW Bartica: 95 m, 17–18 July/1987, C. H. Dietrich; Dietrich Res./14-89-15f ♂; HOLOTYPE/Chiasmodolon/bhagwandorum/Dietrich" (USNM, on indefinite loan from NCSU). Other material: 1 male and 1 female paratype, same data (both NCSU).

Notes.—*C. bhagwandorum* was collected at a blacklight on a forested island in the Mazaruni River, Guyana. The genus name was formed by combining the Greek adjective, *chiasmos,* meaning crosswise, with the masculine noun, *dolon,* meaning dagger, and refers to the crossed knife-like structures on the dorsum of the male pygofer. The species is named in honor of the Bhagwandas family of Bartica, Guyana, whose generous assistance made possible the collection of the type-series.

Behavioral Observations on other Neotropical Idocerinae

We observed ant-attendance in four species of idiocerine leafhoppers, at least two of which are also apparently subsocial. In addition to *Rotundicerus minutus* (discussed above), we observed a female of *Hyalocerus* sp. (S.H.M. lot# 87-133a) with a large aggregation of nymphs being tended by *Crematogaster* sp. ants. Apparently, this leafhopper exhibits subsocial behavior similar to that described for *R. minutus.* Two adult males and several nymphs of a third idiocerine, *Chunroides knighti,* were found in a shelter constructed of decayed plant material by the tending *Azteca* sp. ants on the stem of a small woody shrub with large, ovoid leaves and latex sap. Finally, a female of *Luteobalmus* sp. was observed being tended by ants of the genus *Ectatomma.*

Discussion

While ant-mutualistic and sessile (non-jumping) behavior both appear to correspond with subsociality in the Membracoidea (Membracidae, Aetalionidae, Biturittiidae, and Nicomiidae) and Cicadelloidea (Cicadellidae and Eurymelidae), the pattern of this correspondence differs between the two superfamilies.

As far as is known, all membracoids have sessile nymphs. Sessile behavior assures a relatively stable source of "honey-dew," and thus may have arisen in Membracoidea as a coevolutionary response to the opportunistic ants abundant in lowland, wet tropical forests (Wood 1982, 1984). In some situations, subsociality would subsequently be favored due, as Wood (1984) suggested, to selection for gregarious behavior, because aggregations would provide a more attractive and stable resource for ants. Evidently, ant-attendance was lost in some membracoid groups while their sessile behavior persisted, perhaps facilitated by the evolution of such alternative predator-avoidance strategies as crypsis or aposematic coloration.

In contrast, as far as is known (Beamer and Michener 1950, Evans 1988), most Cicadelloidea have nymphs capable of jumping when disturbed and are neither ant-attended nor subsocial. Thus, while the Eurymelidae and Ulopinae, generally considered to be among the more primitive cicadelloids (Evans 1947, Nielson 1985—see Hamilton 1983 for an alternative classification), have sessile nymphs, suggesting that the ancestral cicadelloid was sessile, this habit was apparently lost early in the evolution of the superfamily. Although most of the cicadellid species in which ant-mutualistic and subsocial behaviors are found belong to subfamilies generally thought to be primitive to moderately primitive (Nielson 1985), their apparent taxonomically disjunct incidence among the Cicadellidae suggests multiple derivations of these behaviors. Further studies of the life-histories of Cicadelloidea, especially of the plesiomorphic groups, are needed to elucidate the relationships among solitary, sessile, gregarious, ant-mutualistic, and subsocial behaviors and their role in the evolution of this group.

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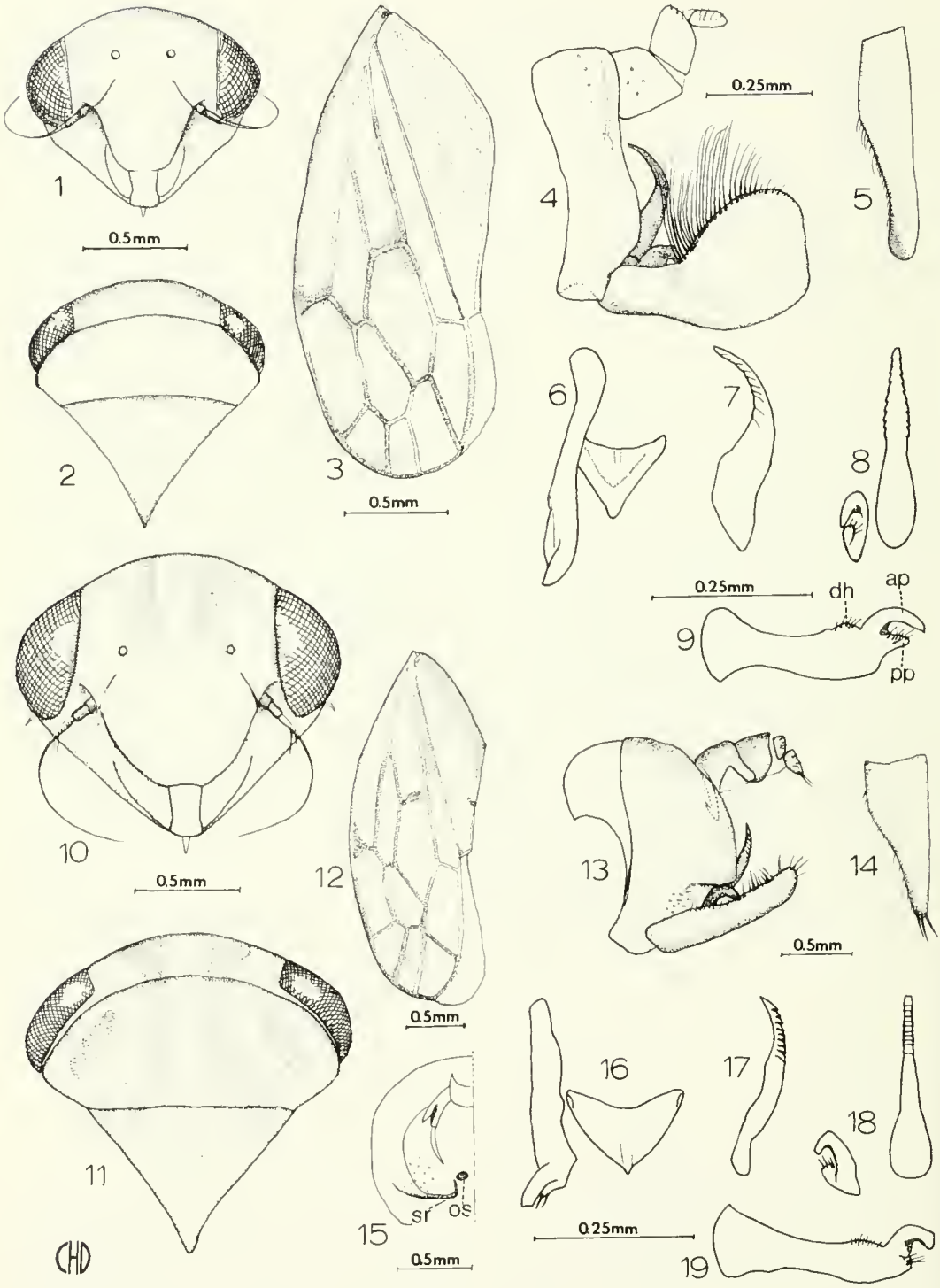
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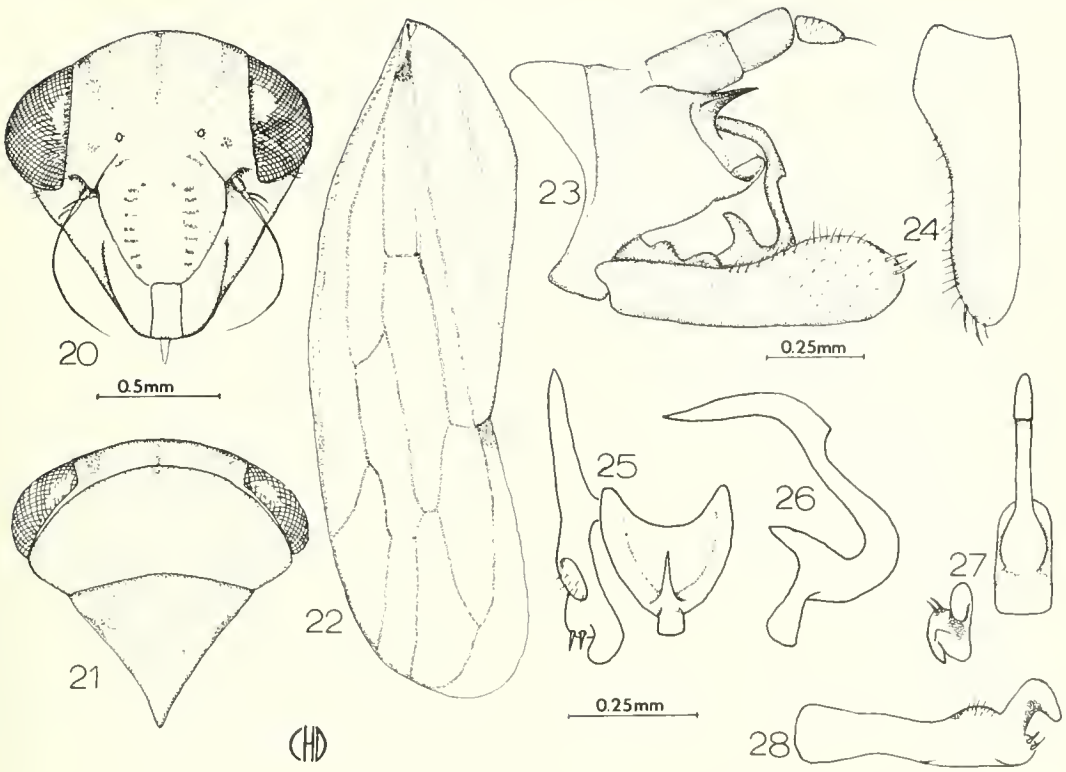

Figs. 20–28. *Chiasmodolon bhagwandorum* Dietrich, new species. 20, Head, anterior view; 21, head, pronotum, and scutellum, dorsal view; 22, left forewing. 23–28 Male genitalia. 23, Genital capsule, lateral view; 24, plate, ventral view; 25, left style and connective, dorsal view; 26, aedeagus, lateral view; 27, aedeagus and left style, posterior view; 28, style, lateral view.

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Figs. 1–19. 1–9, *Rotundicerus minutus* Dietrich, new species. 1, Head, anterior view; 2, head, pronotum, and scutellum, dorsal view; 3, left forewing. 4–9, Male genitalia. 4, Genital capsule, lateral view; 5, subgenital plate, ventral view; 6, left style and connective, dorsal view; 7, aedeagus, lateral view; 8, aedeagus and left style, posterior view; 9, style, lateral view. ap, apical process; dh, dorsal hump, pp, preapical process. Figs. 10–19, *Rotundicerus rubripictus* Dietrich, new species. 10, Head, anterior view; 11, head, pronotum, and scutellum, dorsal view; 12, left forewing. 13–19, Male genitalia. 13, Genital capsule, lateral view; 14, subgenital plate, ventral view; 15, genital capsule (in part), posterior view; 16, left style and connective, dorsal view, 17, aedeagus, lateral view; 18, aedeagus and left style, posterior view; 19, style, lateral view. ha, hooked appendix; os, oval sclerite; sr, sclerotized ridge.

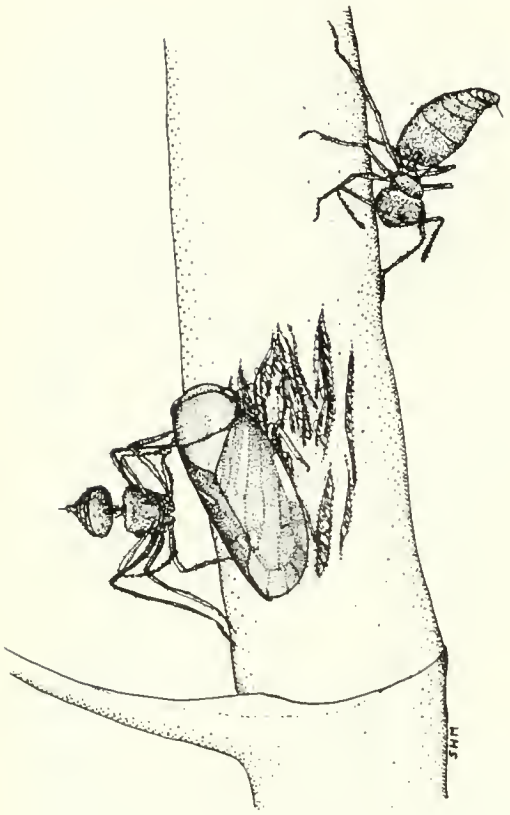

Fig. 29. *Rotundicerus minutus* female, guarding egg mass while tended by *Crematogaster* ants. (Drawn from photograph.)

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92(2), 1990, pp. 224–229

MORPHOLOGY OF THE PUPARIUM OF *LIPOPTENA MAZAMAE* RONDANI (DIPTERA: HIPPOBOSCIDAE)

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Abstract.—The puparium of *Lipoptena mazamae* has an anterior buccal opening with a ventral slit and a posterior region with spiracular pores and an operculated anal area. The spiracular pores have cuticular covering and radiate from each side of the anal area in three curving fields. Each spiracular atrium has a circular opening, minute pegs on the wall, and a tracheal branch beneath. Two triangular, cuticular extensions are situated under the operculum of the anal region. Just below the polygonal area there is an orifice with a collar and an inward cuticular extension. A polygonal pattern that possesses spherical cuticular extensions surrounds the posterior end of the puparium. The remainder of the surface also has a polygonal pattern but with pits on the external and internal surfaces of the cuticle.

Key Words: *Lipoptena mazamae*, Hippoboscidae, puparium, morphology, surface sculpturing, anal opening, respiratory opening

The superfamily Hippoboscoidea (Pupipara) consists of 3 families; Hippoboscidae, Nycteribiidae and Streblidae. The species in these families are obligate ectoparasites and are larviparous. Adult hippoboscids feed on host blood and are known to transmit several parasitic protozoans to domestic and wild birds and mammals (Baker 1967). Bequaert (1953, 1957) gives a detailed description of the anatomy, morphology, biology and evolution of hippoboscids that parasitize mammals and birds. There are several cursory descriptions of the exterior of the puparium of various hippoboscid species (Ferris and Cole 1922, Ferris 1923, 1928, Schruurmans-Stekhoven 1926, Maa 1963, 1969, Theodor 1975). The present study provides a detailed description of the external characteristics of the puparium of *Lipoptena mazamae* Rondani (Diptera: Hippoboscidae).

MATERIALS AND METHODS

Specimens for light and scanning electron microscopy were taken from white-tail deer, *Odocoileus virginianus* Boddaert, in Mississippi. Ten specimens were used for each technique. It was difficult to work with the puparium because of its deep pigmentation and the deleterious effects of leaving the specimens in KOH until the depigmentation is completed. A simple method for depigmentation of fresh or alcohol stored specimens is given here. First specimens were cut in half and placed overnight in a mixture of 3 ml of distilled water, 3 ml of 30% hydrogen perioxide and 0.2–0.3 ml of concentrated ammonium hydroxide (Stapp and Crumley 1936). Next, they were put in 95% ethanol for 30 minutes and then in two changes of absolute ethanol, also for 30 minutes each and cleared in toluene over-

night. Finally the puparia were mounted in a synthetic resin, DPX. Intact puparia were punctured laterally with a minuten. They were put in the depigmenting mixture overnight and then placed in a fresh solution for another 24 h. After dehydration in ethanol the specimens were placed in clove oil for a week. Sometimes the samples had to be placed under a vacuum to facilitate the penetration of the clove oil. Finally the puparia were washed in toluene for 1 h and mounted in Canada balsam.

For scanning electron microscopy fresh or alcohol stored specimens were used. The alcohol stored specimens were rehydrated, then put in 3% OsO_4 for 24 h. They were rinsed for 2 h in four changes of distilled water. After dehydration in ethanol and critical point drying the specimens were attached to aluminium stubs with double-sided sticky tape. The samples were coated with gold-palladium and examined with a Jeol JSM-35CF scanning electron microscope at 20 kV. After the osmication process, several specimens were frozen on dry ice and fractured before further treatment for SEM.

Results

The slightly flattened and oval shaped puparium is 2.3 mm (2.1–2.6 mm) long and 1.9 mm (1.8–2.1 mm) wide (Fig. 1). The anterior end bears a bulge on which the buccal opening is situated and the posterior end bears the spiracular openings and anal operculum (Figs. 1, 3, 5, 11). The buccal opening is circular, with a ventral slit-like extension (Fig. 3).

Just underneath the spiracular and anal region of the posterior end there is a distinct encircling pattern (Fig. 2). The pattern consists of mostly hexagonal polygons with a spherical cuticular extension on each angle (Figs. 2, 4). This pattern is easily observed after the pigmentation is removed. The surface of the rest of the puparium is covered with a similar polygonal pattern (Figs. 4, 10). In addition, there are pits at the angles of each polygon (Fig. 10), and distributed over the inner surface of the polygons (Fig. 8).

Underneath the posterior plate there is a large opening with a distinct collar and surrounding cuticular ridges (Figs. 2, 4, 11). The collar is actually the exposed end of a long internal cuticular extension. Internally there is another collar (Fig. 11 and inset).

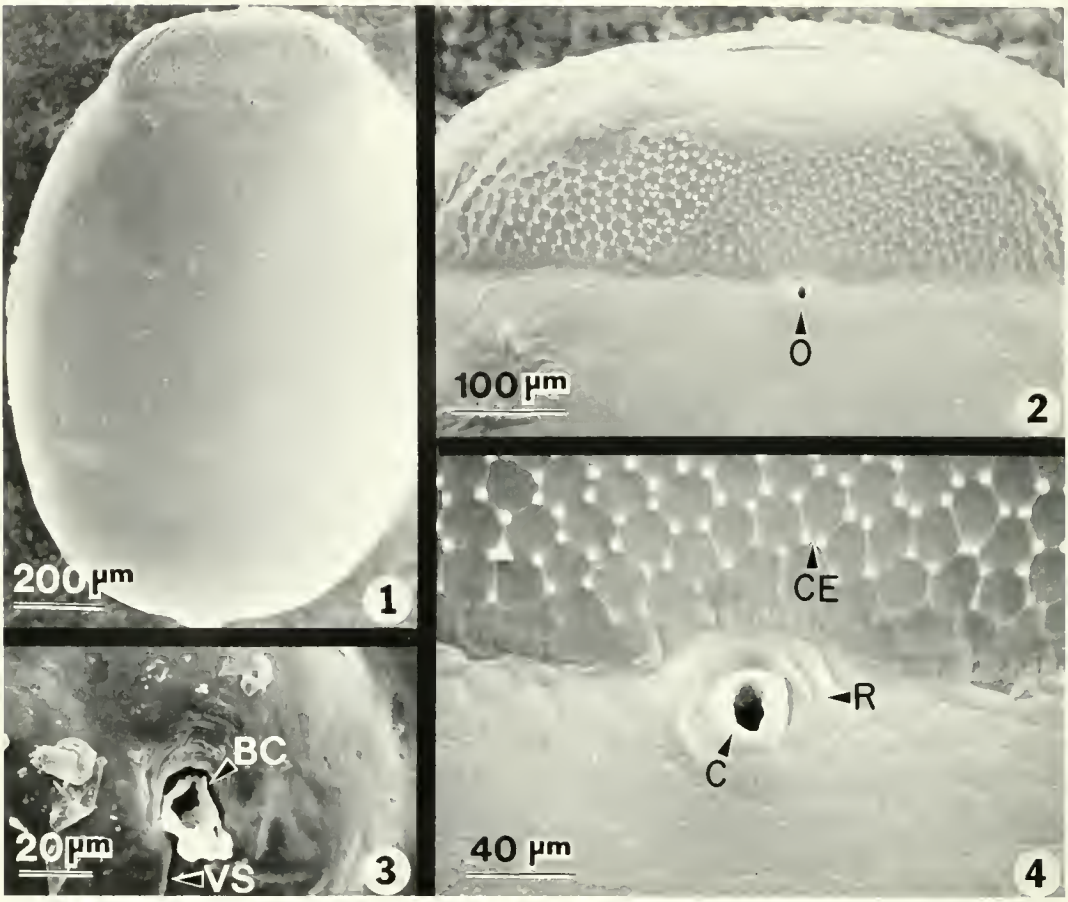
The anal opening, which is situated on the apex of the posterior portion of the body, is hexagonal in shape and has an operculum covers the anal opening (Figs. 5, 11). Beneath the operculum there are two triangular extensions (Fig. 14). Externally the spiracular pores radiate lateral of the anal opening and form three branches on each side with 9, 15 and 17 openings respectively (Figs. 5, 12, 13). Each spiracular pore has an oval-shaped plate with a circular opening (Fig. 6) and under the plate is the slit-like aperture of the atrium (Figs. 7, 8, inset). Inside the atrium there are blunt, oblong projections that line the atrial wall (Fig. 8, inset).

Internally, there is an enlarged portion of the tracheal trunk from which five tracheal branches radiate (Figs. 12, 13). One branch extends back into the body whereas the other four have shorter secondary branches that extend to the spiracular atria (Figs. 7, 8, 12, 13). The internal surfaces of the tracheae have a meshwork of cuticular thickenings (Figs. 7, 9) which maintains shape and provides flexibility to the wall of the tracheae.

Discussion

The size, shape and buccal opening of the puparium is similar in other *Lipoptena* and hippoboscid species (Ferris 1923, 1928, Coatney 1931, Maa 1963, Theodor 1975). According to Bequaert (1953), the developing larva receives its nourishment from the milk glands via the buccal opening.

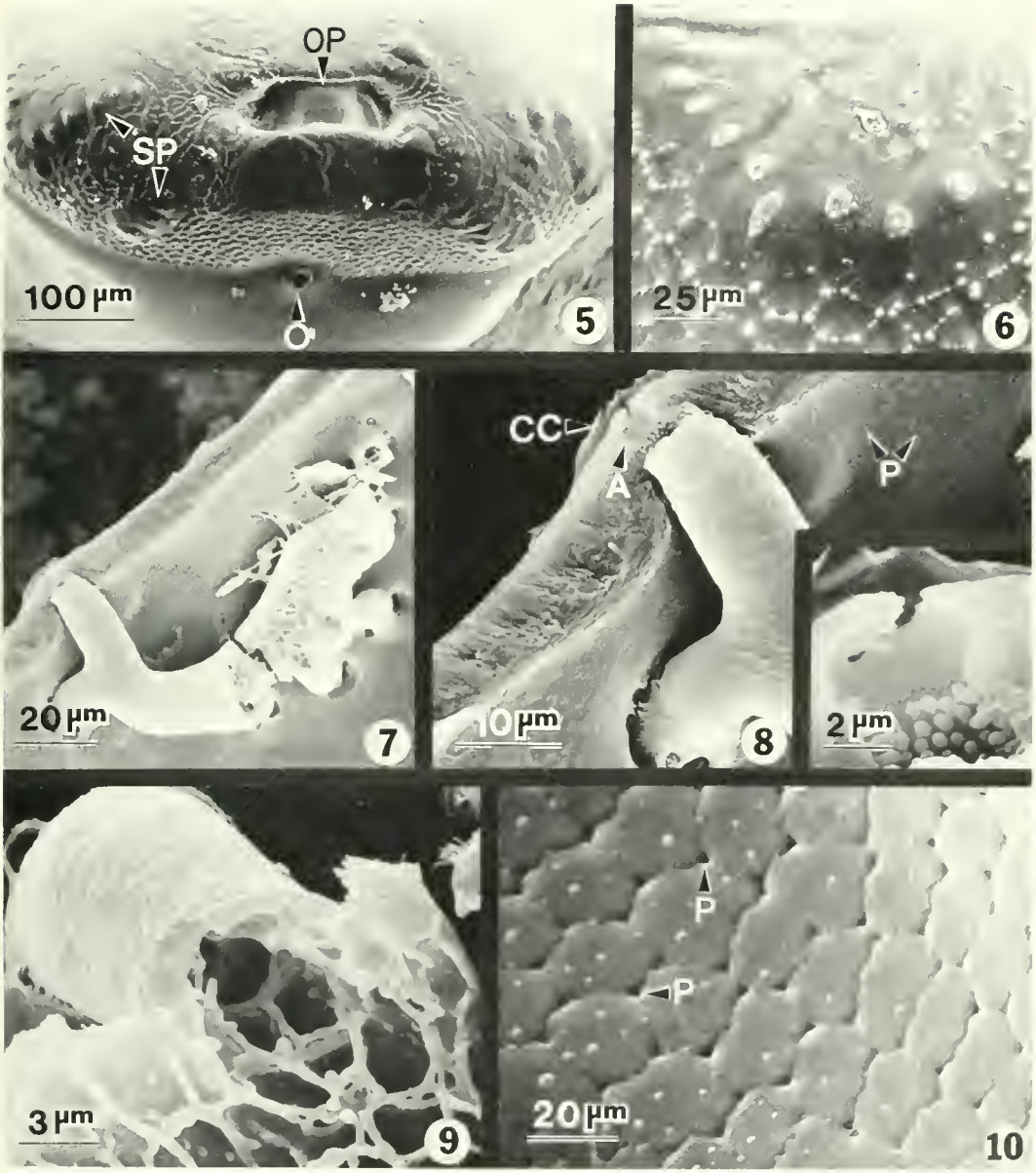
Surface patterns occurs in several genera but the hexagonal pattern with the spherical cuticular extensions that encircles the posterior portion of the puparium in *L. mazamae* is not mentioned in the description



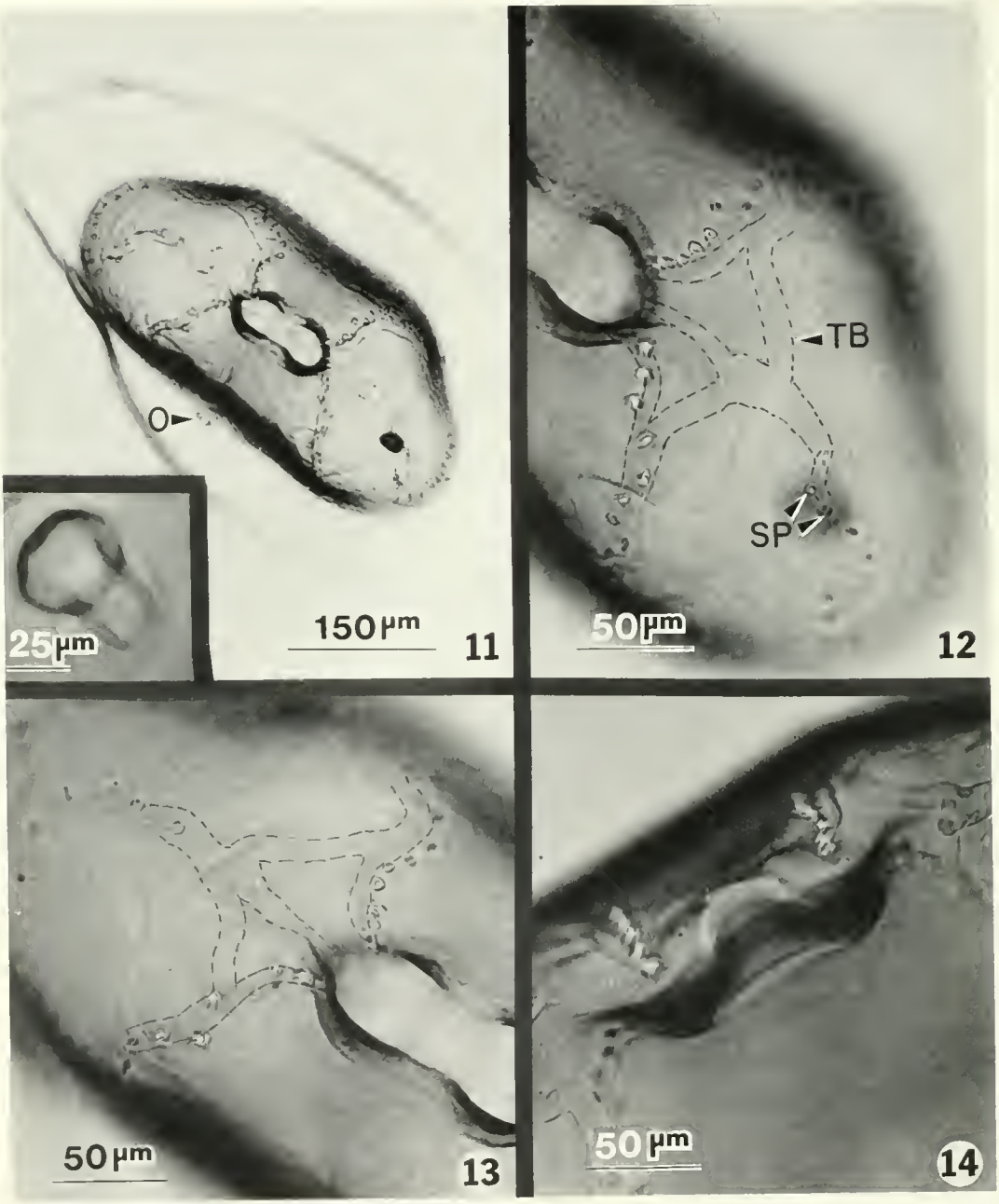
Figs. 1–4. SEM micrographs of the puparium, of *L. mazamae*. 1, Lateral aspect (posterior end shown at top). 2, Posterior region showing the polygonal and orifice (O). 3, Anterior end showing circular buccal cavity (BC) and ventral slit-like extension (US). 4, Higher magnification of Fig. 3 showing circular extension (CE) at the angles of the polygons and the collar (C) and ridges (R) around the orifice.

of a closely related species, *L. depressa*, by Ferris and Cole (1922) and Hearle (1938) or of other genera such as *Pseudolynchia* (Coatney 1931), *Olfersia* (Ferris 1928) and *Hippobosca* (Schruumans-Stekhoven 1926). The rest of the puparium surface in *L. mazamae* has a polygonal pattern with distinct pits. Surface patterning occurs in several genera. Bequaert (1953) observed that the surface in *Stenepteryx* and *Pseudolynchia* are covered with a meshwork of lines whereas in *Stilbometopa* and *Ornitheza* have a punctate surface. The surface in *Olfersia* has straight or hooked spines and short triangular spinules are situated on the surface in *Hippobosca* (Ferris 1928). More research is needed to determine if the differences in surface patterning and sculpturing could be taxonomically important.

Maa (1963, 1969) and Theodor (1975) refer to a large opening below the posterior portion of the puparium as the ventroapical pit, but neither author gives any description of the external area surrounding the opening, or mention the internal cuticular extension. The function of this structure is not known. The shape of the operculum on the anal opening of *L. mazamae* is similar



Figs. 5–10. SEM micrographs of the puparium. 5, Hexagonal operculum (OP) and the arrangement of the respiratory openings (SP). 6, An array of posterior respiratory openings. 7, Tracheal branch under several respiratory openings. 8, Tracheal branch coming from the atrium (A) of the respiratory opening (CC, cuticular covery) (P, pits). Inset, higher magnification of the atrial region, note the peg-like structures on the atrial wall. 9, Inner meshwork of a tracheal branch. 10, Polygonal pattern on the surface of the puparium and the distinct pits (P) associated with the polygons.



Figs. 11–14. Light micrographs of the posterior region of the puparium. 11, Operculum (O) and radiating branches of the tracheal system and the orifice just beneath this region. Inset, the internal cuticular extension of the orifice. 12, 13, Radiating tracheal branches (TB) and respiratory openings laterad of the operculum, (SP, spiracular pore). Dash lines indicate the tracheal branches. 14, Cuticular extension beneath the operculum.

in *Ornithomyia strigilecula* Ferris (Ferris 1923) and in *Hippobosca maculata* Leach (Schruumans-Stekhoven 1926). But previous descriptions of the puparia of *Lipoptena* species do not mention the two triangular extensions beneath the operculum. These structures may be apodemes which attach the muscles that open and close the operculum.

At present there is no description of the external and internal structure of the spiracular pores on the posterior end of a hippoboscid puparium. The outer plate with its narrow opening and the projections on the atrial wall are associated with the tracheal system of other insects and probably act as a filtering system to prevent blockage of the tracheae (Chapman 1982). The internal surface of the tracheae have taenidia which maintain shape and flexibility in the wall of the tracheae (Chapman 1982). The pits on the internal surface of the puparium may be pores that are involved in gas exchange during the pupal stage.

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THE BITING MIDGES OF ALDABRA ATOLL, INDIAN OCEAN (DIPTERA: CERATOPOGONIDAE)

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Abstract.—Eighteen species of biting midges are recorded from Aldabra Atoll, Indian Ocean, of which three are described as new: ***Dasyhelea cogani, D. hutsoni,*** and ***Culicoides adamskii*** **SPP. N.** These and two previously described species, *Forcipomyia hutsoni* Wirth and Ratanaworabhan and *Metacanthohelea cogani* Wirth and Grogan, are endemic to Aldabra. The low degree of endemism (27%) in the Aldabra midges is contrasted with the Seychelles species, where 37 of 43 species are endemic (86%). Although incomplete collections make these figures tentative, they can partially be explained by the Seychelles' geographic isolation and elevationally varied habitats, in contrast with Aldabra's position relatively close to the African continent and elevationally uniform, low atoll environment.

Key Words: biting midges, Ceratopogonidae, Aldabra Atoll

The biota of the islands and atolls of the Indian Ocean has interested naturalists and geographers since the earliest European explorations reported the occurrence of large flightless birds and giant tortoises (Abbott 1893). Studies of the insect fauna have lagged far behind and it is only in recent years that comprehensive collections have been made. One striking exception was the Percy Sladen Trust Expedition to the Indian Ocean in 1905–1909, the entomological results of which were summarized by Scott (1933). More recently Legrand (1965) reported comprehensively on the Lepidoptera that he collected on the Seychelles and Aldabra from 1956 to 1960.

Beginning in 1966 the Royal Society of London established a scientific research station on Aldabra Atoll and began extensive collections. A comprehensive report on their research was published under the editorship of Westoll and Stoddart (1971). Preliminary studies on the affinities and composition of the insect fauna of Aldabra were published as a part of this report by Cogan et al. (1971). Peake (1971) also presented his analysis of the evolution of terrestrial faunas in the western Indian Ocean as part of this report. Later, Stoddart and Westoll (1979) edited a comprehensive report on the terrestrial ecology of Aldabra, in which Frith (1979) summarized a 12-month study of insect abundance and composition on the atoll.

Brian Cogan and Tony Hutson sent me their 1967 Aldabra biting midge collections (Diptera: Ceratopogonidae) for study in 1969, but I was reluctant to publish promptly because the ceratopogonid fauna of the western Indian Ocean islands, Madagascar, and the adjacent African continent was so poorly known. In the meantime Wirth et al. (1980) catalogued the Subsaharan Ceratopogonidae, and several important papers were published, among which the following deserve mention: Clastrier (1959) on the biting midges of Réunion, de Meillon (1961) on Madagascar, and Wirth and Messersmith (1977) and Clastrier (1983) on the Seychelles. Frith (1979) reported that her trap collections in several localities included large numbers of Ceratopogonidae but these were not identified further, and it was not

Table 1. Numbers of genera, species, endemic species, and percent endemism in Ceratopogonidae of certain western Indian Ocean land masses.

	Number of Genera Reported	Number of Species Reported	Number of Endemic Species	Percent Endemism
Entire Afrotropical Region (Wirth et al. 1980)	34	622	NA[a]	NA
Madagascar (de Meilion 1961)	12	31	10	32%
Seychelles (Clastrier 1983)	14	43	37	86%
Réunion (Clastrier 1959)	5	15	5	33%
Aldabra (present study)	7	18	5	27%

[a] Not applicable.

possible to sort them out from their bulk storage in the British Museum (Nat. Hist.) and include them in the present study. David Adamski of Starkville, Mississippi, collected on Aldabra Atoll in 1986, producing a good collection of midges that he took at light, which has been included in this study.

Previously only three species of biting midges were recorded from Aldabra Atoll: *Forcipomyia hutsoni* Wirth and Ratanaworabhan (1976), *Dasyhelea nigricans* Carter, Ingram & Macfie and *Stilobezzia spirogyrae* Carter, Ingram & Macfie (reported in Wirth et al. 1980). In the present study I report 18 species in seven genera from Aldabra, of which three species were previously undescribed and five are endemic to Aldabra.

A comparison with the number of genera, species, and endemic species reported elsewhere in the western Indian Ocean and Subsaharan Region as a whole is given in Table I. As stated above, a fair comparison cannot be made, since so little is known of the Madagascar fauna, but one cannot fail to be impressed by the high degree of endemism (86%) in the species of the isolated, high elevation, Seychelles Islands compared with the low endemism (27%) in the low Aldabra Atoll which lies closer to the African continent.

The systematic arrangement used here follows that given in the Subsaharan Catalogue by Wirth et al. (1980), except that following Wirth and Grogan (1988) the tribes Ceratopogonini and Stilobezziini are combined in one tribe, the Ceratopogonini. Keys to the genera may be found in Wirth et al. (1974). Explanation of the taxonomic characters used can be found in the general papers on Ceratopogonidae by Wirth (1952) and Downes and Wirth (1981).

Holotypes of material collected by Cogan and Hutson are deposited in the British Museum (Natural History), London (BMNH); that collected by Adamski is in the National Museum of Natural History, Smithsonian Institution, Washington (USNM). Some paratypes, and other material as specified, are deposited in the Museum National d'Histoire Naturelle in Paris (PARIS).

Adamski's Aldabra material was collected by permission of Mr. Lindsay Chong-Seng, Ministry of Development and Natural Resources, Victoria, Mahe, Republic of Seychelles, and under the auspices of the Smithsonian Institution Expedition to Aldabra Atoll (1986), Dr. Brian Kensley, Smithsonian Institution, Leader. The Kenya specimens of *Forcipomyia vesicula* de Meillon & Wirth were made available by Professor D. S. Kettle from material collected by Dr. R. Harmsen on the University College Nairobi, Mount Kenya Expedition, March 1966.

Subfamily Forcipomyiinae

Forcipomyia (*Forcipomyia*) *callithorax* (Kieffer), 1911.

Ceratopogon lasionotus var. *callithorax* Kieffer, 1911: 335 (♂, ♀; Seychelles).

Forcipomyia lasionota var. *callithorax* (Kieffer); Ingram & Macfie, 1924: 545 (combination; in key).

Forcipomyia (*Forcipomyia*) *callithorax* (Kieffer); Clastrier, 1983: 39 (redescribed; figs.; Seychelles, from types).

Diagnostic characters.—A small, pale brown, unmarked species with pale yellowish legs. Female: Wing length 0.90 mm; costal ratio 0.46; hind tarsal ratio 1.00. Wing without pale markings, macrotrichia long and abundant on costa and radius, less prominent on rest of wing; halter pale. Antenna pale brown; antennal ratio (11–15/3–10) 1.10. Palpus pale brown; lengths of segments in proportion of 12-22-58-25-22; third segment swollen to tip with small, deep pit; palpal ratio 2.0. Mandible slender, hyaline and distally pointed, with a distal series of microscopic teeth too fine to be counted, possibly 20–30 in series. Body without short broad striated scales. One spermatheca present; elongate with long tapering neck; measuring 0.124 by 0.072 mm.

Distribution.—Aldabra, Seychelles.

Material examined.—ALDABRA ATOLL: West Island (Ile Picard), Settlement, 12–22.iii.1986 (*D. Adamski*), 1 ♀ (USNM).

Forcipomyia (*Forcipomyia*) *vesicula* de Meillon & Wirth, 1983.

Forcipomyia (*Forcipomyia*) *vesicula* de Meillon & Wirth, 1983: 350 (♂, ♀; South Africa; figs.).

Diagnostic characters.—A moderately large, stout, dull, pale brown species with unmarked wing and legs; mesonotum with three broad, obscurely darker brown vittae. Female: Wing length 1.1–1.5 mm; costal ratio 0.45. Antenna brown, distal segments scarcely elongated, antennal ratio 0.75. Palpus yellowish, becoming brownish distally; third segment slightly swollen on proximal half; palpal ratio 2.7. Hind tarsal ratio 1.0. Spermathecae two, large, slightly unequal, measuring 0.340 by 0.144 mm and 0.270 by 0.125 mm; faintly pigmented, bladder-like, ovoid to spindle-form in shape, with short, slender, abruptly bent necks. Male: Genitalia yellowish, contrasting with dark brown proximal abdominal segments; aedeagus pale, shape as usual in the subgenus; parameres pale, with bases fused in a broad plate to a third of total length, stout and slightly sinuate distally, apices tapered to a fine point slightly curved laterad.

Types.—Augrabies Falls, Gordonia Dist., Cape Province, SOUTH AFRICA, 27–28.x.1980, (de Meillon & Van Eeden) (type in Natal Museum).

Distribution.—Aldabra, Kenya, South Africa.

Material examined.—ALDABRA ATOLL: South Island; Cinq Cases, 3–16.i.1968, at light, 1 ♀; Takamaka Pool, 1–17.ii.1968, at light, 2 ♂, 2 ♀ (Cogan & Hutson) (BMNH); West Island (Ile Picard), Settlement, 12–22.1986 (D. Adamski), UV light trap, 15 ♂, 24 ♀ (BMNH, USNM, PARIS: Mississippi State Mus.). KENYA: Mt. Kenya, 3900 m, 19.iii.1966 (R. Harmsen), reared from lower woody stem of decayed *Lobelia keniensis*, 1 ♂, 2 larvae, 1 pupal exuviae (BMNH).

Forcipomyia (*Lepidohelea*) *lepidota* Ingram & Macfie, 1924.

Forcipomyia lepidota Ingram & Macfie, 1924: 566 (♂, ♀; Gold Coast; figs.); Clastrier, 1956: 506 (redescribed; figs.; Tunisia, Algeria); Dessart, 1961: 362 (redescribed; figs.; synonymy); Dessart, 1963: 82 (redescribed; figs.; synonymy).

Diagnostic characters.—A dark brown species with banded legs including a median yellowish band on hind femur. Hind tarsal ratio of female 0.90, of male 0.82. Male genitalia with dististyle swollen distally with very characteristic, obliquely capitate expansion; aedeagus also with specifically diagnostic distal expansion, the basal arch very low, nearly transverse; parameres separate, the long posterior processes tapering to slender, slightly sinuate rods.

Distribution.—Widespread in Subsaharan and Oriental Regions.

Material examined.—ALDABRA ATOLL: South Island; Dune Jean-Louis, 13–20.iii.1968, 1 ♀; Takamaka Grove, 1–17.ii.1968, 1 ♂ (USNM), 1 ♀ (BMNH), (Cogan & Hutson).

This species has been very well redescribed and figured by Clastrier (1956) and Dessart (1961). According to Clastrier (1983), *Forcipomyia chrysolopha* (Kieffer) is a distinct species readily distinguished by the stouter, straight, posterior processes of the parameres and by the stouter, non-tapering, distal portion of the aedeagus.

Forcipomyia (*Microhelea*) *fuliginosa* (Meigen), 1818.

Ceratopogon fuliginosus Meigen, 1818: 86 (Germany).

Forcipomyia fuliginosa (Meigen); Goetghebuer, 1933: 130 (combination; Congo); Wirth, 1956: 357 (distribution; insect feeding records; synonymy); Dessart, 1963: 63 (redescribed; Africa; figs.; synonymy); Wirth, 1972: 567 (redescribed; figs.; synonymy; distribution; Neotropical records).

Distribution.—Worldwide.

Material examined.—ALDABRA ATOLL: South Island, Takamaka Pool, 1–17.ii.1968, (Cogan & Hutson), 1 ♀ (BMNH).

This species is a widely distributed, common parasitic species sucking haemolymph from a wide variety of smooth-bodied caterpillars and sawfly larvae, especially larvae of Sphingidae. Closely resembling species of the subgenus *Forcipomyia*, but with short basitarsi (tarsal ratio about 0.50); third palpal segment elongate and swollen nearly to tip, with deep pit extending nearly the length of segment; palpal segment 4 much longer than 5; mandible with numerous (30–35) fine teeth; and the male parameres fused for nearly half of total length.

Forcipomyia (*Pterobosca*) *hutsoni* Wirth & Ratanaworabhan, 1976.

Forcipomyia (*Pterobosca*) *hutsoni* Wirth & Ratanaworabhan, 1976: 242 (all stages; Aldabra; figs.).

Types.—Holotype ♀, ALDABRA ATOLL, South Island, Cinq Cases, 3–16.i.1968, (Cogan & Hutson) (BMNH). Paratypes, 59 ♀, 1 ♂, 22 larvae, 2 pupae, same data (BMNH, USNM).

Distribution.—Aldabra.

Forcipomyia hutsoni was described from material collected by Cogan and Hutson on Aldabra. Most of the females were attached to the wings of dragonflies from which meals of haemolymph are taken; the male was collected at light, and the presumed larvae and pupae were collected in leaf axils of *Pandanus*. Of the related species of the subgenus *Pterobosca*, the closest is *Forcipomyia ariel* (Macfie), known only from the Moluccas in Indonesia.

Subfamily Dasyheleinae

Dasyhelea fenerivensis de Meillon, 1961.

Dasyhelea fenerivensis de Meillon, 1961: 12 (♂, Madagascar; fig. genitalia).

Type.—Holotype ♂, Fenerive, Madagascar, xii.1955, B. Stuckenberg, at light on beach (in Inst. Rech. Sci. Madagascar).

Distribution.—Aldabra, Madagascar.

Material examined.—ALDABRA ATOLL: South Island, Takamaka Grove, 1–17.ii.1968, 1 ♂ (USNM); Frigate Pool, 20.i.1968, 1 ♂ (BMNH) (all Cogan & Hutson).

This species belongs to the *Dasyhelea nigricans* Group and is readily separable from all other members of the group by the bifid apex of the posterior projection of the parameres. *Dasyhelea borbonica* Clastrier (1959) from Réunion is similar but has the ninth sternum produced caudad over the aedeagus in a blunt point, the paramere has a slender tip with a short slender subapical projection, the aedeagus is not so strongly sclerotized on the lateral margins, and the

dististyle bears a slender, distally directed, mesal process near the base.

Dasyhelea inconspicuosa Carter, Ingram & Macfie, 1921.

Dasyhelea inconspicuosa Carter, Ingram & Macfie, 1921: 191 (all stages; figs.; Ghana).

Diagnostic characters.—A small, dark brown species with yellowish scutellum, brownish legs, and infuscated halteres. Wing length 0.7–0.9 mm; costal ratio 0.43; macrotrichia long and abundant. Female spermatheca small (0.032 mm diameter) and subspherical with a short neck (0.005 mm). Male genitalia nearly as broad as long, ninth tergum with slender apicolateral processes; ninth sternum with narrow median projection over base of aedeagus; aedeagus with small, strongly sclerotized, transverse basal sclerite, a small rounded black median sclerite, and a short slender pair of submedian processes with slender tips hooked ventrad. Parameres with stout, slightly asymmetrical basal apodemes, the median posterior process poorly developed.

Distribution.—Widespread in Subsaharan Region from Ghana to Mozambique and the Sudan; Aldabra.

Material examined.—ALDABRA ATOLL: South Island, Dune Jean-Louis, 13–20.iii.1968, at light (Cogan & Hutson), 2 ♂ (BMNH, USNM).

Dasyhelea monosticta (Ingram & Macfie), NEW COMBINATION

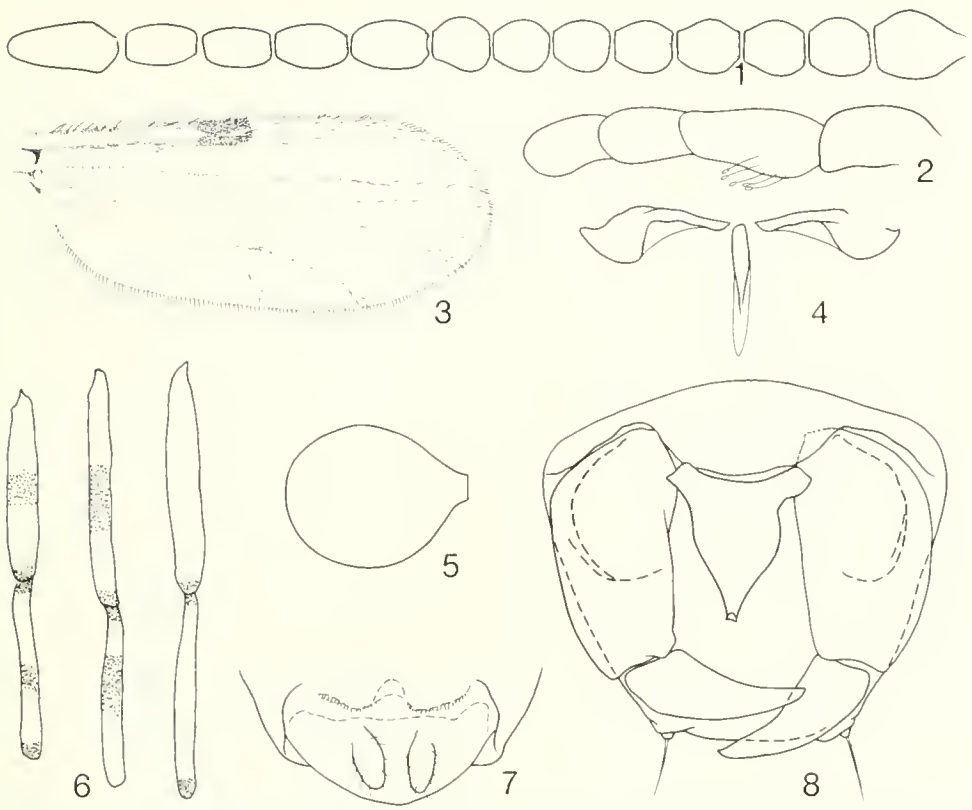
Thysanognathus monostictus Ingram & Macfie, 1923: 60 (♀; Zanzibar; figs.); Macfie, 1938: 159 (compared with *Dasyhelea atronotata* Macfie from Solomon Islands; ? *Dasyhelea*).

Alluaudomyia monosticta (Ingram & Macfie); de Meillon, 1939: 9 (combination; in key).

Types.—Four ♀ syntypes, ZANZIBAR, Prison, 1.xii.1918 (Dr. W. M. Aders) (BMNH). Dr. John Boorman in March 1980 examined and photographed three ♀ syntype slides (two more or less complete specimens and one with a wing only) which appear to be all that remain of the type series. Selected photographs of these syntypes shown in Figs. 9–13 indicate without doubt that the species belongs in the genus *Dasyhelea* (NEW COMBINATION). They also indicate that our Aldabra material is conspecific, and I can now supplement the original description and add the description of the hitherto unknown male.

Female.—Wing length 0.83 mm; breadth 0.36 mm; costal ratio 0.48. A small, pollinose, pale brown species with faint brownish vittate markings on mesonotum, and scutellum dark in middle. Legs (Figs. 6, 11) whitish with black knee spots and moderately distinct brownish bands on midportions of fore and mid femora and tibiae; extreme apices of tibiae and all tarsomeres slightly infuscated. Wing (Figs. 3, 10) whitish hyaline, a single dark brown spot on anterior margin over second radial cell, the latter well formed; macrotrichia sparse and pale, scarcely distinguishable. Halter with white knob. Antenna (Fig. 1) pale brown; short and stout, proximal segments nearly moniliform, no sharp break in length between 10 and 11; lengths of flagellar segments in proportion of 30-22-20-20-20-20-20-20-22-22-20-20-41; segments with proximal reticulations; antennal ratio 0.74; last segment with blunt tip. Palpus (Fig. 2) short and stout; lengths of segments in proportion of 19-24-14-14. Abdomen brownish with narrow pale segmental bands; genital sclerotization (Fig. 7) a small transverse brownish plate surrounding gonopore, with slender, sinuate lateral arms. Spermatheca (Fig. 5) one, ovoid with short tapering neck; small, measuring overall 0.036 by 0.029 mm.

Male.—Wing length 0.88 mm; breadth 0.33 mm; costal ratio 0.46. Similar to the female with the usual sexual differences. Antenna with sparse brownish plume extending to segment 12; segments 3–12 more or less fused; lengths of flagellar segments in proportion of 35-22-18-18-18-18-18-18-



Figs. 1–8. *Dasyhelea monosticta*. 1–3, 5–7 female; 4, 8 male: 1, antenna; 2, palpus; 3, wing; 4, parameres; 5, spermatheca; 6, femora and tibiae of (left to right) fore, mid and hind legs; 7, genital sclerotization; 8, genitalia, parameres omitted.

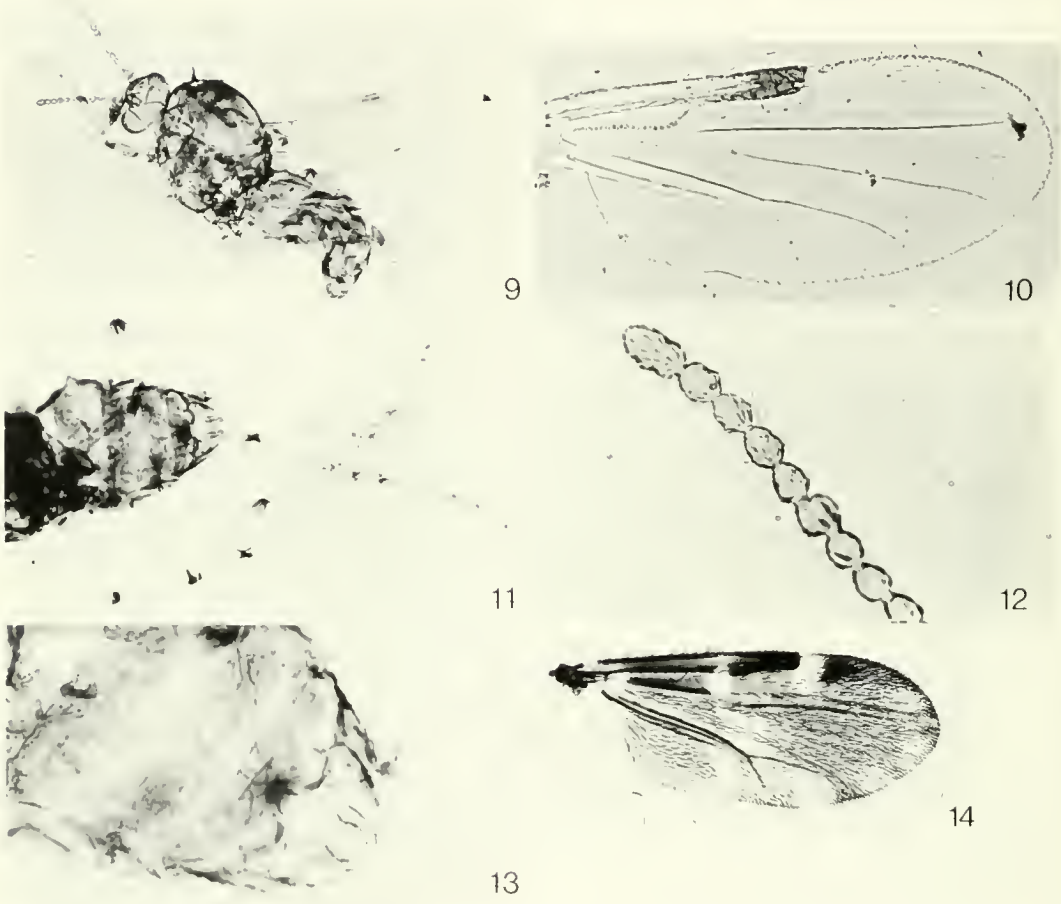
18-36-33-33-50, antennal ratio (12-15/3-11) 0.83. Palpus with lengths of segments in proportion of 11-10-30-20. Genitalia (Fig. 8) slightly broader than long, in ventral view nearly circular in outline because of the rounded ninth tergum which lacks distinct apicolateral processes; ninth sternum narrow with mesal expansion to base of aedeagus; basistyle about twice as long as broad, slightly tapering distally; dististyle short, stout at base, tapering abruptly to pointed tip; aedeagus shield-shaped, slightly longer than basal breadth, well sclerotized on anterior margin with short, stout lateral arms, tapering distally with convex lateral margins to slender tip bent ventrocaudad. Parameres (Fig. 4) symmetrical; basal apodemes rather stout laterally, only slightly bent, tapering mesad to slender junction with the small, slender, straight, rodlike posterior process with pointed tip.

Distribution.—Aldabra, Zanzibar.

Material examined.—ALDABRA ATOLL: South Island, Point Hodoul, 21.i.1968, large tidal solution hole, 10 ♀, 200 ♂; same, swarming in large tidal solution hole, approximately 1000 ♂, ♀; same, 27.i.1968, tidal saline pool, 2 ♂, 5 ♀ (all Cogan & Hutson) (BMNH, USNM, PARIS).

Dasyhelea nigricans Carter, Ingram & Macfie, 1921.

Dasyhelea nigricans Carter, Ingram & Macfie, 1921: 194 (♂; Ghana; fig. genitalia);



Figs. 9–13. *Dasyhelea monosticta*, female syntypes frrom Zanzibar: 9, whole mount; 10, wing; 11, abdomen and legs; 12, antennal segments 7–15; 13, distal abdominal segments. Fig. 14, *Culicoides adamskii*, wing of female paratype.

Ingram & Macfie, 1921: 328 (♀; Nigeria); Clastrier, 1959: 417 (♂ redescribed; fig. genitalia; Réunion); Clastrier & Wirth, 1961: 321 (redescribed; Gambia; figs.).

Distribution.—Aldabra, Ethiopia, Gambia, Ghana, Nigeria, Réunion, Transvaal.

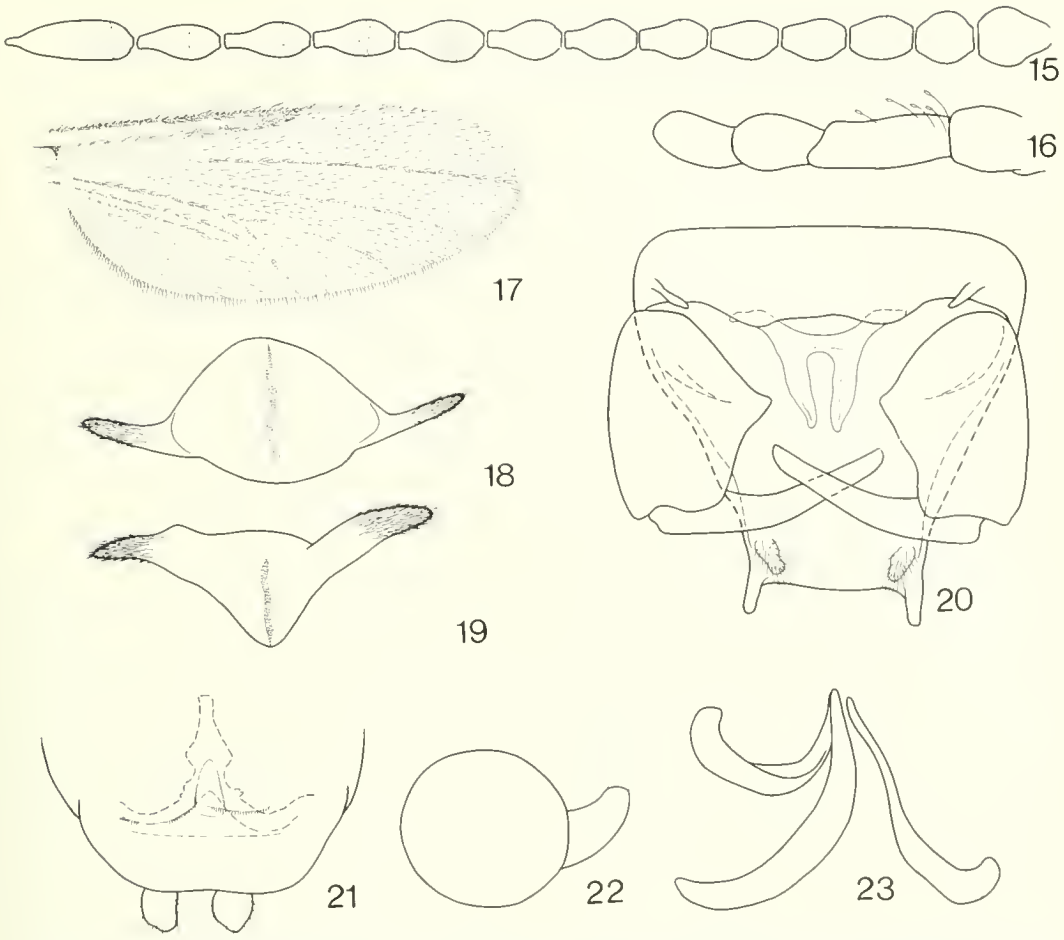
Material examined.—ALDABRA ATOLL: South Island, Cinq Cases, 23–29.i.1968, (Cogan & Hutson), 1 ♂, 1 ♀ (BMNH).

This small dark species is recognized by its yellow legs and deeply two-pronged male dististyle.

Dasyhelea speciosa Clastrier, 1983

Dasyhelea speciosa Clastrier, 1983: 34 (♀; Seychelles; figs.)

Diagnostic characters.—Wing length 1.10–1.20 mm; costal ratio 0.56. A moderately large dark brown species with bluish-green pollinose thorax; scutellum yellowish, brownish in center. Legs yellowish brown with blackish knee spots and faint, broad, median brownish bands on femora and tibiae. Halter infuscated. Wing (Fig. 17) with abundant macrotrichia; second radial cell



Figs. 15–23. *Dasyhelea speciosa*; 15–18, 21–22, female; 19–20, 23, male: 15 antenna; 16, palpus; 17, wing; 18, 19, precoxal bridge; 20, genitalia, parameres omitted; 21, genital sclerotization; 22, spermatheca; 23, parameres.

lenticular; end of costa oblique. Antenna (Fig. 15) with all flagellar segments moderately elongated and tapering, more so toward apex; last segment with distinct terminal appilla; flagellar segments with distinct coarse reticulations (plaques) proximad of the verticils, distal portions of segments 11–15 without pubescence. Palpus (Fig. 16) moderately stout. Precoxal bridge (Fig. 18 female, Fig. 19 male) an oval to somewhat triangular transverse sclerite with ends elongated and tapered and bearing dense pubescence. Female subgenital plate (Fig. 21) with undulating caudolateral arms and anteromedian projection elongated with distinct basal constriction. Spermatheca (Fig. 22) ovoid to subspherical, measuring 0.080 by 0.076 mm, with long oblique slender neck measuring 0.043 mm long. Male genitalia (Fig. 20, 23) indistinguishable from that described by Wirth & Messersmith (1977) for *D. seychellensis* (Kieffer).

Types.—Clastrier (1983) designated as holotype the specimen from Beau Vallon, Mahe, Seychelles, 25.iv.1963, (Tams & Nye) (BMNH) from a series of four females from

the same locality with different dates that had been described and figured by Wirth & Messersmith (1977) under the name *D. seychellensis* (Kieffer).

Distribution.—Aldabra, Seychelles.

Material examined.—ALDABRA ATOLL: South Island, Cinq Cases, 3–16.i.1968, 1 ♂; Dune Jean-Louis, 13–20.iii.1968, shoreline on beach, 1 ♂, 1 ♀; Takamaka, 1–17.ii.1968, 3 ♂, 3 ♀. West Island, near Settlement, 21–31.iii.1968, at light, 1 ♂; Ile Picard Settlement, 12–22.iii.1986 (D. Adamski), 1 ♀. ASTOVE ATOLL: Coconut Plantation, 5.iii.1968, 2 ♂, 1 ♀. (All Cogan & Hutson except as noted; BMNH, USNM, PARIS.)

Kieffer (1911) described *D. seychellensis* from two specimens from Mahe, Seychelles: One female, Cascade Estate, about 1000 feet and over; and one male, Cascade Estate, about 800–1500 feet, 1909. Wirth and Messersmith (1977) selected the male as lectotype and described and figured the genitalia. They described and figured the female of the species from four females collected by Tams and Nye at Beau Vallon, Mahe, 12–30.iv.1965. Clastrier (1983) in his revision of the Seychelles Ceratopogonidae found that Kieffer's original female from Cascade Estate differed markedly (as outlined in his key) from the females described by Wirth & Messersmith, and described as *D. speciosa* sp. n. the Tams and Nye specimens, along with three females collected by Brown, on Silhouette, Seychelles. The Aldabra females reported here agree perfectly with the female of *D. speciosa* Clastrier, but the associated males cannot be separated from the male lectotype of *D. seychellensis* described by Wirth & Messersmith. It is possible that the female described by Clastrier as *D. speciosa* is the true female of *D. seychellensis* and that the Kieffer's female described by Clastrier as *D. seychellensis* is another unnamed species, but it is also possible that the males of the two species are indistinguishable. Further collections are necessary to resolve the possible synonymy.

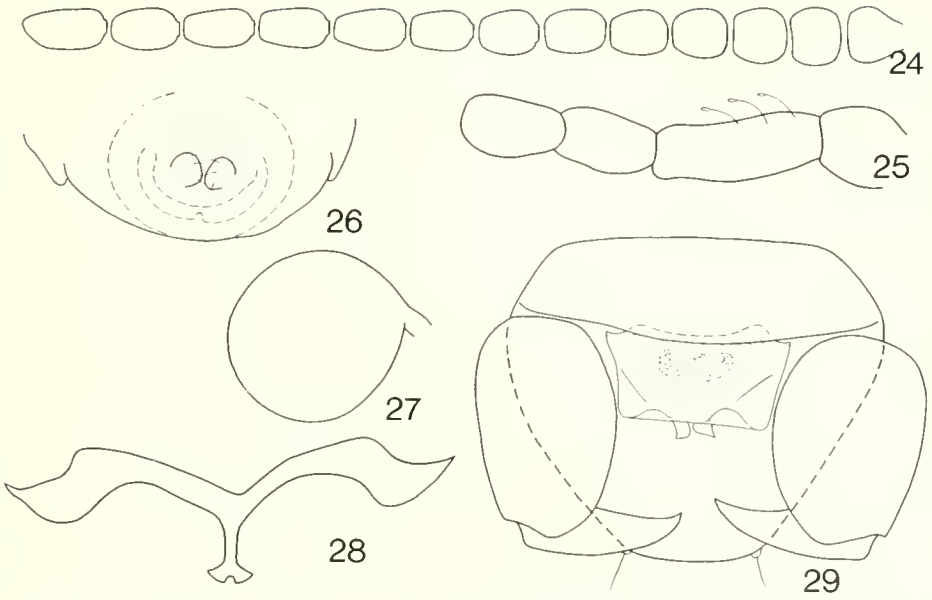
Females of *D. Seychellensis* and *D. speciosa* can be Separated as Follows:

1. Antennal segments 11–15 without microscopic pubescence, with very prominent reticulations (plaques) proximad of the verticils; anterior process of subgenital plate elongate and narrowed at the base; spermatheca retort-shaped with oblique, long slender neck . . . . . *speciosa* Clastrier
– Antennal segments 11–15 with microscopic pubescence present their entire length; plaques poorly formed proximad of the verticils; anterior process of subgenital plate short with parallel margins; spermatheca subglobose to pyriform . . . . . *seychellensis* (Kieffer)

Dasyhelea cogani Wirth, New Species

Female allotype.—Wing length 0.64 mm, breadth 0.32 mm; costal ratio 0.46. A very small, intensely dark brown species with brownish legs and halteres, and smoky pale brownish wings. Antenna (Fig. 24) short and stout; flagellar segments in nearly continuous series, lengths of segments in proportion of 21-16-16-17-17-17-17-17-20-20-20-20-25, antennal ratio 0.76; last segment bluntly pointed. Palpus (Fig. 25) short and stout, lengths of segments in proportion of 12-26-17-20. Hind tarsal ratio 2.6. Mesonotum dark brown, scutellum yellowish brown. Wing short and broad, smoky brownish, veins brown; macrotrichia long and coarse, moderately dense, arrangement in sparse rows; first radial cell vestigial, second slitlike. Abdomen dark brown, pleural membrane with black microsetae arranged in close-set, microscopic rows. Genital sclerotization (Fig. 26) in form of an anteromedian sclerotized loop with slender caudolateral arms. Spermatheca (Fig. 27) one, well pigmented, subspherical; small, measuring 0.033 mm in diameter, with a short, slender, oblique neck 0.007 mm long.

Male holotype.—Wing length 0.81 mm; breadth 0.32 mm; costal ratio 0.50. Similar to female with the usual sexual differences; larger and more slender; wing with second



Figs. 24–29. *Dasyhelea cogani*; 24–27, female; 28–29, male: 24, antenna; 25, palpus; 26, genital sclerotization; 27, spermatheca; 28, parameres; 29, genitalia, parameres omitted.

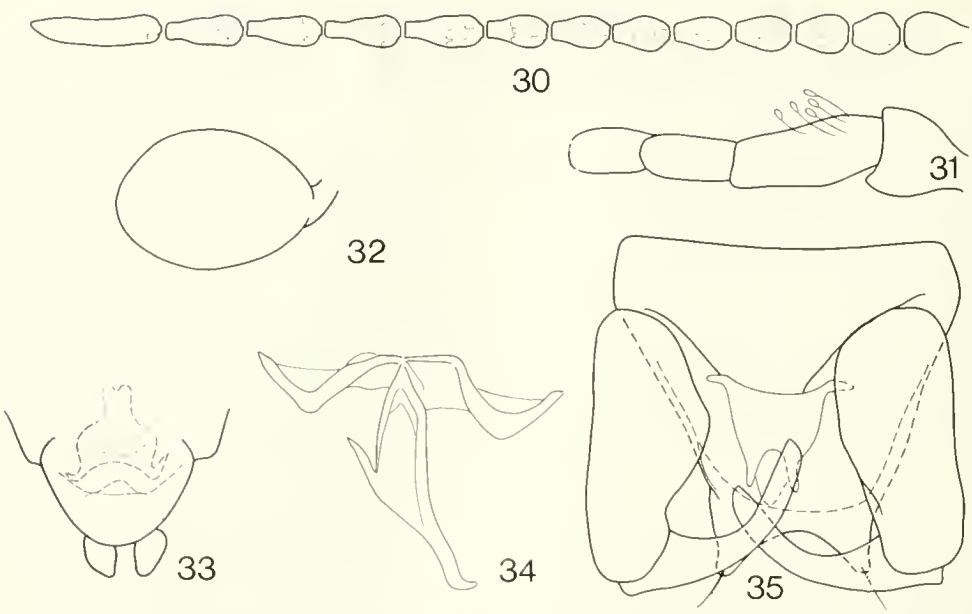
radial cell open; legs with longer vestiture. Antenna with dense plume of long brown verticils extending to segment 14, segments 3–12 more or less fused; lengths of flagellar segments in proportion of 35-26-22-22-22-23-23-25-25-56-56-48-50, antennal ratio (12–15/3–11) 0.97. Hind tarsal ratio 2.2. Genitalia (Fig. 29): Short and broad, much broader than long; ninth sternum with straight caudal margin; ninth tergum rounded caudally without distinct apicolateral processes. Basistyle short and stout, with patch of strong setae on ventromesal face near apex; dististyle short and stout, slightly curved and tapering distally to a sharp point. Aedeagus with narrow, sclerotized anterior bar joining short lateral arms; main body a transverse, quadrate, sclerotized plate ventrally, a pair of short, distally attenuated, sclerotized processes extending caudally from basal bar, their apices closely approximated, and dorsomost, a small, somewhat arcuate, transverse sclerite. Parameres (Fig. 28) symmetrical, basal apodemes irregularly arched anteriorly, becoming more slender mesad and joining on midline and giving rise to a slender posterior process with a small, expanded, buttonlike, slightly bilobed tip.

Distribution.—Aldabra, Astove Atolls.

Types.—Holotype ♂, 1 ♀ paratype, ASTOVE ATOLL: Around coconut plantation, 5.iii.1968, (Cogan & Hutson) (BMNH). ALLOTYPE ♀ (BMNH), 2 ♂, 6 ♀ paratypes, ALDABRA ATOLL: South Island, Cinq Cases, 3–11.i.1968, (Cogan & Hutson) (BMNH, PARIS, USNM).

This species is dedicated to Brian Cogan, formerly of the British Museum (Nat. Hist.), in recognition of his interest in collecting the fine series of Aldabra Ceratopogonidae and in appreciation of his long and lasting friendship.

Dasyhelea cogani is closely related to *D. latiforceps* Clastrier (1983) from the Seychelles. The latter species differs mainly in the shape of the female spermatheca which is irregularly oval with stout neck, the genital sclerotization which has a stout, angulate anterior loop, male paramere which has



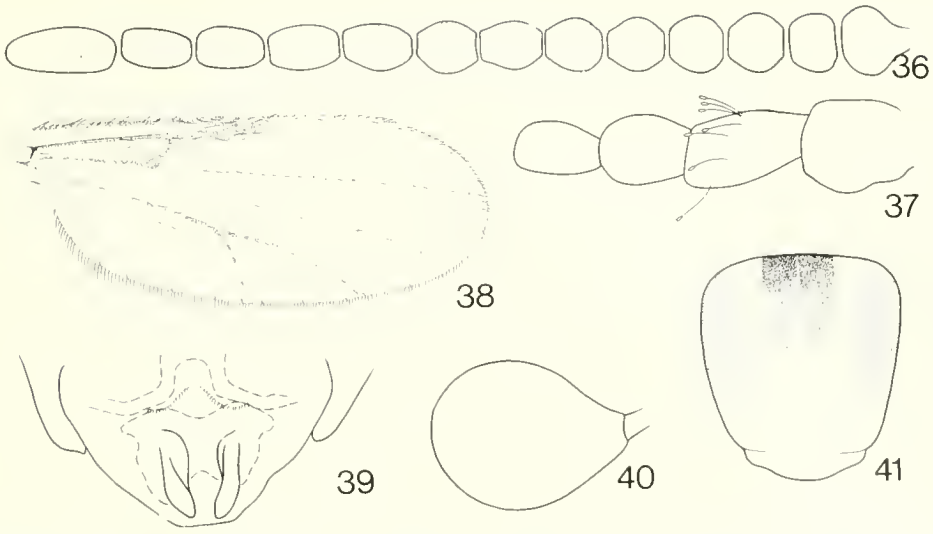
Figs. 30–35. *Dasyhelea hutsoni*; 30–33, female; 34–35, male; 30, antenna; 31, palpus; 32, spermatheca; 33, genital sclerotization; 34, parameres; 35, genitalia, parameres omitted.

a spoonlike rather than bifurcate tip, and aedeagus which has the lateral sclerites much more slender and lacks the dorsal arcuate sclerite.

Dasyhelea hutsoni Wirth, New Species

Female holotype.—Wing length 0.66 mm; breadth 0.31 mm; costal ratio 0.52. Head pale brown, antennae darker brown. Antenna (Fig. 30) with lengths of flagellar segments in proportion of 27-22-23-25-25-25-26-27-36-34-32-34-56, antennal ratio 0.96; segments sculptured proximally, last segment elongate with tapering tip. Palpus (Fig. 31) short and relatively stout, lengths of segments in proportion of 19-30-15-12. Thorax pale brown, scutellum and sides of mesonotum yellowish; legs uniformly stramineous. Hind tarsal ratio 3.0. Wing smoky grayish, veins slightly darker; macrotrichia moderately numerous over entire wing, long, coarse and dark brown; first radial cell vestigial, second well formed, square-ended. Halter brownish. Abdomen brownish; genital sclerotization as in Fig. 33; spermatheca (Fig. 32) one, well pigmented; oval with short oblique neck; measuring 0.054 by 0.026 mm and neck 0.009 mm long.

Male allotype.—Wing length 0.78 mm; costal ratio 0.48. Similar to the female, with the usual sexual differences. Antenna with sparse plume of long brown verticils; segments 7–12 fused; flagellar segments with lengths in proportion of 30-25-23-23-23-23-23-23-23-50-50-50-62, antennal ratio (12–15/3–11) 0.98. Palpus with lengths of segments in proportion of 15-30-16-17. Hind tarsal ratio 2.4. Genitalia (Fig. 35): Ninth sternum with evenly rounded posterior convexity abutting base of aedeagus; ninth tergum short and tapering, about as long as basal breadth, apicolateral processes a pair of angular lobes ending in a somewhat beadlike setigerous process, the caudal margin between the lobes deeply concaved. Basistyle somewhat swollen proximally, with-



Figs. 36–41. *Dasyhelea tamsi* female: 36, antenna; 37, palpus; 38, wing; 39, genital sclerotization; 40, spermatheca; 41, mesonotal pattern.

out special lobe or armature; dististyle about as long as basistyle, base only moderately enlarged, tapering and curved distally to moderately stout, pointed tip. Aedeagus of diagnostic shape; deeply pigmented; main body slightly broader than long, anterior margin slightly concave, with short, slender anterolateral arms; posteriorly a pair of short, stout processes tapering to blunt tips slightly turned ventrolaterad. Parameres (Fig. 34) with stout, slightly asymmetrical basal apodemes; posterior median portion swollen on proximal half with a short, strongly pigmented, slender, pointed process abruptly bent back ventrolaterad from near midlength; distal half strongly narrowed to a pointed tip directed ventrolaterad to side opposite the proximal process.

Types.—ALDABRA ATOLL: holotype ♀, allotype ♂, 4 ♂ and 1 ♀ paratypes; South Island, Takamaka Pool, 1–17.ii.1968, (Cogan & Hutson), at light; 1 ♀ paratype, Takamaka, in mangroves, otherwise same data. Ile Michel, 16.ii.1968, (Cogan & Hutson), 1 ♀ paratype. (Holotype and allotype in BMNH; paratypes in BMNH, PARIS, USNM.)

Distribution.—Aldabra.

This species is dedicated to A. M. Hutson of the Department of Entomology, British Museum (Nat. Hist.), London, in appreciation of his interest and assistance in my study of the Aldabra Ceratopogonidae.

Dasyhelea hutsoni closely resembles *D. labourdonnaisi* Clastrier (1959) from Ile Réunion in general appearance and in the structure of the male aedeagus, but the related species differs in its larger size (male wing length about 1.2 mm), straight caudal margins of the ninth sternum and tergum, the apicolateral processes of the tergum long and slender; the aedeagus with longer anterolateral arms; the dististyle tapering to more slender tip; the posterior portion of the paramere shorter and evenly tapered to the tip and lacking the retrorse proximal process, and the basal apodemes very slender and asymmetrical.

Dasyhelea tamsi Wirth & Messersmith, 1977.

Dasyhelea tamsi Wirth & Messersmith, 1977: 305 (♀; Seychelles; figs.); Clastrier, 1983: 36 (♀ redescribed from type series).

Diagnostic characters.—A small pollinose pale gray species; wing whitish with slightly darkened stigma. Mesonotum (Fig. 41) pale brown with three broad dark brownish gray vittae, humeri extensively pale yellowish gray; on slide-mounted specimens five narrow opaque lines of internal pigmentation form borders to the vittae (as noted by Clastrier 1983). Scutellum yellowish. Legs whitish, knee spots blackish. Antenna (Fig. 36) short, with segments in a continuous series, moniliform proximally to slightly elongate on distal segments, last segment without terminal stylet; surface of segments conspicuously reticulated. Palpus (Fig. 37) short and stout. Wing (Fig. 38) milky whitish, radial cells forming a dark stigma; costa ratio 0.49; veins forming radial cells greatly strengthened, the first radial cell obsolete, second short with small lumen; macrotrichia long and stout, very sparse, forming lines along veins. Halter grayish infuscated. Abdomen grayish brown, terga with pairs of small round hyaline nonpigmented spots. Genital sclerotization (Fig. 39) with slightly infuscated, quadrate, median lobe and a slender pair of oblique lateral arms. Spermatheca (Fig. 40) one, ovoid, tapering to short stout neck; heavily sclerotized; small, measuring 0.060 by 0.045 mm. Male unknown.

Distribution.—Aldabra, Seychelles.

Material examined.—ALDABRA ATOLL: South Island, Dune Jean-Louis, 13–20.iii.1968, at light, 2 ♀; Anse Cedre, 17–19.i.1968, 1 ♀; Takamaka Grove, 1–17.ii.1968, 1 ♀ (all Cogan & Hutson) (BMNH, PARIS, USNM). West Island (Ile Picard), Settlement, 12–22.iii.1986 (D. Adamski), 23 ♀ (USNM).

Subfamily Ceratopogoninae

Tribe Culicoidini

Culicoides adamskii Wirth, New Species

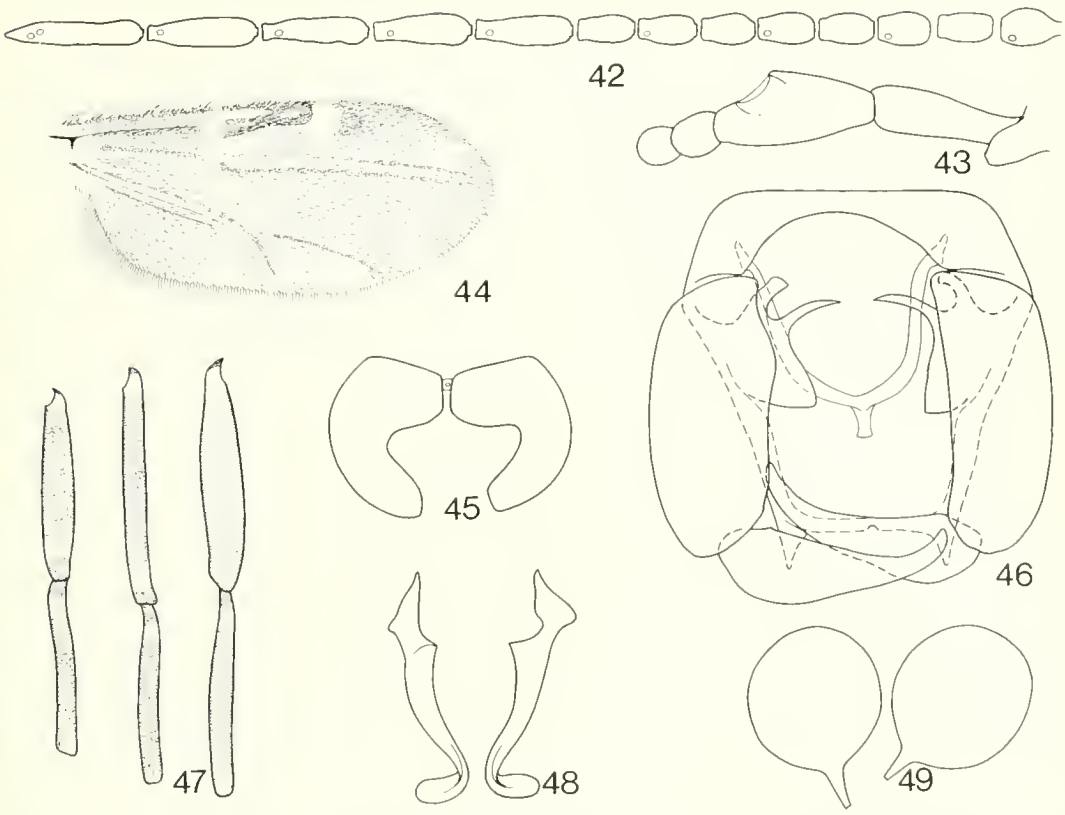
Female holotype.—Wing length 1.16 mm; breadth 0.55 mm; costal ratio 0.58.

Head: Brown, antennal flagellum yellow. Eyes (Fig. 45) bare, narrowly separated, by width of ½ facet. Antenna (Fig. 42) with lengths of flagellar segments in proportion of 35-24-26-26-27-28-27-30-50-50-50-57-75, antennal ratio 1.25; sensilla coeloconica present on segments 3, 5, 7, 9, 11–15. Palpus (Fig. 43) dark brown; lengths of segments in proportion of 15-50-55-22-22; third segment moderately swollen distally, with a moderately large, round, moderately deep sensory pit; palpal ratio 2.02. Proboscis moderately long; P/H Ratio 0.79. Mandible with 16 teeth.

Thorax: Brown; mesonotum subshining dark brown with grayish pollinosity; three dark brown vittae, a narrow median vitta on anterior half, a pair of broad sublateral bands from humeral pits to above wing bases; a pair of small dark brown spots in prescutellar depression. Legs (Fig. 47) dark brown, knee spots blackish; fore and mid femora with subapical, and all tibiae with sub-basal, narrow pale rings, tarsi pale; hind tibial comb with five spines, second from spur longest.

Wing (Fig. 14, 44): Strongly infuscated, veins dark brown. Pattern as figured; two prominent but small pale spots on anterior margin, first over r-m crossvein continued cephalad to costal margin, second just past tip of costa and extending caudad half the width of cell R5; faint rounded pale spots at wing margin in each of cells R5, M1, M2, and M3+4, the latter filling distal half of cell; small pale spot at wing base just distad of basal arculus; a faint pale spot in cell M2 just behind medial fork and another just in front of mediocubital fork; anal cell with a double pale spot distally extending broadly to posterior wing margin. Macrotrichia long and coarse, abundant, covering entire wing; radial cells well-formed, with distinct lumens. Halter dark brown.

Abdomen: Brown. Spermathecae (Fig. 49) two plus sclerotized ring and vestigial third; subequal, spherical with long slender necks; each measuring 0.087 by 0.087 mm plus neck 0.032 mm long.



Figs. 42–49. *Culicoides adamski*; 42–45, 47, 49, female; 46, 48, male; 42, antenna; 43, palpus; 44, wing; 45, eye separation; 46, genitalia, parameres omitted; 47, femora and tibiae of (left to right) fore, mid and hind legs; 48, parameres; 49, spermathecae.

Male allotype.—Similar to female with usual sexual differences. Genitalia (Fig. 46): Ninth sternum with broad, shallow, caudomedian excavation, ventral membrane not spiculate; ninth tergum about as long as basal breadth, tapering to small, pointed, moderately separate, apicolateral processes, the caudal margin between them straight, with only a hint of a median notch. Basistyle about twice as long as broad, with unusual modification of mesal margin consisting of a broad, distally pointed, platelike basal lobe extending from ventral root to half the length of basistyle; ventral root long and slender, slightly curved; dorsal root curved, half as long, with blunt tip; dististyle somewhat swollen proximally, gradually tapering distally to slender, incurved tip. Aedeagus with basal arms slender and evenly curved, forming a high slender arch to ⅕ of total length; distal process small and slender, with simple tip. Parameres (Fig. 48) each with strong basal knob bearing a short anterior process, constricted a short distance just past knob; mid portion nearly straight, slightly bowed outwardly, gradually tapering distad, the short distal portion abruptly bent ventrolaterad and slightly expanded in a rounded, flattened, spoonlike tip.

Distribution.—Aldabra.

Types.—ALDABRA ATOLL: Holotype ♀, West Island (Ile Picard), Settlement, 12–22.iii.1986, (D. Adamski), in UV light trap (USNM). Allotype ♂, South Island, Dune Jean-Louis, 13–20.iii.1968 (Cogan & Hutson) (BMNH). Paratypes, 7 ♂, 36 ♀, as fol-

lows: Same data as holotype, 1 ♀; same data as allotype, 4 ♂, 4 ♀ (BMNH, PARIS, USNM). South Island, Dune D'Messe, 21.iii.1968, (Cogan & Hutson), 21 ♀; Takamaka, 1–17.ii.1968 (Cogan & Hutson), 1 ♂, 7 ♀. Middle Island, near East Channel, 6–7.ii.1968, (Cogan & Hutson), 1 ♀. West Island, near Settlement, 21–31.iii.1968, (Cogan & Hutson), 1 ♂, 1 ♀ (BMNH, PARIS, USNM).

This species is dedicated to David Adamski of Mississippi State University, who sent me a small but important collection of Aldabra Ceratopogonidae for study.

Culicoides adamskii is closely related to *C. eriodendroni* Carter, Ingram, & Macfie (1921) and *C. nigripennis* Carter, Ingram & Macfie (1920), the taxonomy of which is still in some confusion, with a number of closely related mainland Subsaharan species in the complex remaining to be described (Cornet, Glick, Meiswinkel, Phelps, in litt.). *C. adamskii* resembles *C. nigripennis* in antennal sensillar pattern 3,5,7,9,11–15, palpal proportions and shape of the sensory pit, shape and size of the spermathecae, leg color pattern and dark halter, but differs markedly in wing pattern which in *C. nigripennis* is restricted to two small anterior pale spots, and the longer costa (costal ratio 0.64) and presence of only four tibial spines in *C. nigripennis*. *Culicoides eriodendroni* resembles *C. adamskii* in wing pattern, leg pattern, and dark halter, but has antennal sensillar pattern 3,11–15, four tibial spines, and unequal ovoid spermathecae without necks.

The male genitalia of *C. nigripennis* (as figured by Boorman & Dipeolu 1979) resemble those of *C. adamskii* but have the dististyle like that of *C. eriodendroni*, basistyle like that of *C. lamborni* Ingram & Macfie (1925), and the parameres are more slender than in either species and lack the spoonlike swelling at the tip. The male genitalia of *C. eriodendroni* (as figured by Ingram & Macfie 1921) differ in the large basal swelling on the dististyle, lack of the basal lobe on the mesal margin of the basistyle, and shorter, stouter parameres. *Culicoides lamborni*, known from the male only, has a wing pattern like that of *C. nigripennis*, and the genitalia have the dististyle and aedeagus like those of *C. adamskii*, but the parameres have a slender apex and the basistyle lacks the basal lobe.

The described species of the *C. nigripennis* Group have been reared from rot holes in various trees, and it is reasonable to expect to find the immature stages of *C. adamskii* in similar habitats.

Tribe Ceratopogonini

Metacanthohelea cogani Wirth & Grogan, 1988.

Metacanthohelea cogani Wirth & Grogan, 1988: 66 (♂, ♀; Aldabra; figs.).

Diagnostic characters.—A small, dull dark brown midge; wing length 0.90 mm. Eyes broadly separated, bare. Female antenna with distal five segments elongated; distal three segments of male antenna elongated; male antennal segments 3–10 fused, with sparse plume. Palpus 5-segmented; third segment short, swollen, with well-defined sensory pit. Legs moderately stout; hind femur swollen, bearing 14 large spines on distal half; fourth tarsomeres short but subcylindrical, bearing single apical sinuate hyaline sensillum; female claws small and equal with basal inner teeth. Wing milky, with two narrow radial cells, second 1.5 times length of first; costal ratio 0.67; vein M2 narrowly interrupted at base. Two ovoid spermathecae with oblique long slender necks. Aedeagus triangular, broad and short; parameres fused basally with long slender distal portions recurved at their tips.

Distribution.—Aldabra, Kenya.

Types.—ALDABRA ATOLL: Holotype ♀, allotype ♂, South Island, Takamaka, 1–17.ii.1968, (Cogan & Hutson) (BMNH). Paratypes, 2 ♂, 2 ♀, same data; 1 ♂, South Island, Dune Jean-Louis, at light, 13–20.iii.1968 (Cogan & Hutson); 1 ♂, West

Island, near settlement, at light, 21–31.iii.1968 (Cogan & Hutson). One ♀ paratype, KENYA, Marsabit Nature Reserve, 4200 ft, 8.xii.1969 (Irwin & Ross) (California Acad. Sci.).

Material examined.—ALDABRA ATOLL: West Island (Ile Picard); Settlement, 12–22.iii.1986, (D. Adamski), 1 ♂ (USNM).

The occurrence of this highly modified genus and species in only two widely disjunct localities.—The Indian Ocean atoll of Aldabra, and at 1250 m elevation at the Marsabit Nature Reserve in Kenya, has interesting biogeographical implications which at present are not readily explained, except to point out the close relationship of the Aldabra fauna to that of the African mainland.

Stilobezzia spirogyrae Carter, Ingram & Macfie, 1921.

Stilobezzia spirogyrae Carter, Ingram & Macfie, 1921: 325 (all stages; Ghana; figs.).

Distribution.—Aldabra, Gambia, Ghana, São Tome, South Africa.

Material examined.—ALDABRA ATOLL: Ile Michel, 3.ii.1968, 1 ♂. South Island, Cinq Cases, 3–16,23–29.i.1968, 4 ♀; Flamingo Pool, 21–22.i.1968, 10 ♀; Frigate Pool, 20,i.1968, 1 ♂; Takamaka, Takamaka Grove, Takamaka Pool, 1–17.ii.1968, 76 ♂, 23 ♀ (all Cogan & Hutson) (BMNH, PARIS, USNM).

Tribe Sphaeromiini

Homohelea stuckenbergi (de Meillon), 1961.

Sphaeromias stuckenbergi de Meillon, 1961: 51 (♀; Madagascar; figs.).

Homohelea stuckenbergi (de Meillon); Wirth et al. 1980: 170 (combination); de Meillon & Wirth, 1981: 543 (in key).

Distribution.—Aldabra, Madagascar.

Material examined.—ALDABRA ATOLL: South Island, Cinq Cases, 23–29.i.1968, 2 ♀; Frigate Pool, 20.i.1968, 1 ♀; Takamaka, 1–17.ii.1968, 2 ♀ (all Cogan & Hutson) (BMNH, PARIS, USNM).

This species is distinguished from its Subsaharan congeners by its large size (wing length more than 3.0 mm), ornamented mesonotum and abdomen, fore femur with 9 spines, mid and hind femora with 4–6 spines, and only one talon of the fore claws barbed.

Tribe Palpomyiini

Bezzia africana Ingram & Macfie, 1923

Bezzia africana Ingram & Macfie, 1923: 71 (♀; South Africa; figs.); de Meillon, 1943: 107 (♂; Transvaal; figs.); Haeselbarth, 1975: 357 (redescribed; figs.; distribution; synonymy)

Distribution.—Aldabra, Cameroun, Madagascar, South Africa, Zimbabwe.

Material examined.—ALDABRA ATOLL: South Island, Takamaka Pool, 1–17.ii.1968, (Cogan & Hutson), 1 ♂.

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BIOLOGY OF *OBEZA FLORIDANA* (ASHMEAD) AND *PSEUDOCHALCURA GIBBOSA* (PROVANCHER) (HYMENOPTERA: EUCHARITIDAE)

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Abstract.—Brief descriptions of life history are given for *Obeza floridana* (Ashmead) and *Pseudochalcura gibbosa* (Provancher) from Florida and northern Ontario, respectively. *Obeza floridana* oviposits into fruits of *Cyanococcus simulatus* Small and *P. gibbosa* into overwintering floral buds of *Ledum groenlandicum* Oeder. and leaf buds of *Arbutus menziesi* Pursh. Descriptions of eggs and first-instar larvae of each species are provided and compared to other Eucharitidae. *Pseudochalcura gibbosa* was reared from *Camponotus herculeanus* (L.) and details of complete life history and descriptions of all larval stages are supplied. Comparisons are made with the Old World genus *Stilbula* and their taxonomic interrelationships discussed.

Key Words: life history, larval stages

Obeza floridana (Ashmead) and *Pseudochalcura gibbosa* (Provancher) belong to the family Eucharitidae (Hymenoptera: Chalcidoidea). The genus *Obeza* Heraty was recently erected to hold the New World species that were previously considered to be members of the widespread Old World genus *Stilbula* Spinola (Heraty 1985). The genus *Stilbula*, and the genera *Obeza*, *Lophyrocera* Cameron (considered here to include *Tetramelia* Kirby) and *Pseudochalcura* Ashmead comprise a monophyletic group (Heraty 1985, 1986).

Systematic relationships within this clade have already been discussed (Heraty 1985, 1986) and are summarized as follows. *Obeza* has been regarded as the sister group to *Lophyrocera* + *Pseudochalcura* while *Stilbula* was considered the sister taxon to these three New World genera (Heraty 1985). *Lophyrocera* was again recognized as a sister group to *Pseudochalcura* by Heraty (1986) although this was questioned at the time. Exact placement of the genus *Pseudochalcura* is problematic since it is the only member lacking lateral propodeal processes and short, bifurcating spines issuing from the frenum. Close taxonomic relationship between *Pseudochalcura* and *Obeza* or *Stilbula* is supported by synapomorphies which include similar structure of the pronotal-prepectal area and musculature of the mesosoma (Heraty 1989). A recent discovery of two undescribed species of *Pseudochalcura* from the Orient suggest a closer relationship to the Old World genus *Stilbula* and to the recently described genus *Stilbuloidea* Bouček. Exact systematic relationships of these taxa have yet to be assessed but the monophyly of the group is certain (Heraty 1986).

As with other members of the Eucharitidae, the above-mentioned genera are specialized parasites of mature larvae and pupae of ants. Adult females deposit their eggs

away from the host into plant tissue. The active first-instar larva, termed a planidium, must make its way back to the ant nest, usually phoretically on an adult ant, where it can attack the brood (Clausen 1940a, b, 1941). Morphology of the immature stages, and in particular, the well-sclerotized planidium, is highly conservative and can be useful in positing relationships at the higher taxonomic levels (Heraty and Darling 1984). Such an approach can serve to test, supplement, and refine hypotheses derived from studies of adult morphology.

Lophyrocera (including *Tetramelia*) includes six described Neotropical species and *L. apicalis* Ashmead in the western United States (Heraty 1985). Nothing is known of the biology or immature stages of any of these seven species.

The genus *Obeza* is widespread in South America with two species represented in North America: *Obeza septentrionalis* (Brues) in Arizona and New Mexico and *O. floridana* in Florida and Georgia (Heraty 1985). The biology and immature stages of *Obeza* have remained completely unknown until this time.

Pseudochalcura is also widely distributed in the Neotropics (ten species) with three other species occurring in the Nearctic (Heraty 1986). *Pseudochalcura gibbosa* is widespread in North America and has a typical Boreal distribution to the north and occurs throughout the Rocky Mountains in the west (Heraty 1986). Adults of *P. gibbosa* have been recorded as ovipositing into flower buds of *Gossypium* (Malvaceae) in Arizona (Pierce and Morrill 1914) and *Arbutus* (Ericaceae) in California, along with collecting associations made with various other plants (Heraty 1986). *Pseudochalcura gibbosa* has been reared from *Camponotus novaeboracensis* (Fitch) in Michigan (Wheeler 1907), *Camponotus laevigatus* (F. Smith) and *Camponotus* sp. possibly *vicinus* Mayr in California (Heraty 1986). The only description of immature stages of *P. gibbosa* was by Wheeler (1907) for the female pupa and position of two pupae in a cocoon of *C. novaeboracensis*.

In contrast to the paucity of information on the biology of the New World genera discussed here, there are detailed life history documentations and descriptions of immature stages for *Stilbula cyniformis* Rossi (Parker 1932, 1937, Parker and Thompson 1925), *Stilbula manipurensis* (Clausen) (Clausen 1928, 1940a, b), and *Stilbula tenuicornis* (Ashmead) (Clausen 1923, 1940b, 1941). Some peculiar features in the life histories of *Stilbula* species are useful in distinguishing this group from other Eucharitidae and for comparison to the two species in this paper. Females deposit their large egg masses of more than one thousand eggs in a single oviposition, and in *S. tenuicornis* and *S. cyniformis*, the eggs have the ability to overwinter (Clausen 1928, 1940b, Parker 1937). As in other eucharitids, planidia are mobile and attach themselves externally to mature ant larvae. The first-instar larvae are unique in their ability to complete development on the mature larva within the cocoon, and in *S. tenuicornis*, are cast off with the host's larval exuvium. The second-instar larvae then relocates to the mid-section of the pupa to resume feeding (Clausen 1923, Parker 1928). Finally, the third-instar larva has a distinctive morphology with respect to other known genera of Eucharitidae, and more than one eucharitid can develop on a single host pupa (Clausen 1923, 1940a, Parker 1932). The recorded ant hosts include *Camponotus herculeanus japonicus* Mayr and *Camponotus herculeanus obscuripes* Mayr for *S. tenuicornis* (Clausen 1923, 1941), *Camponotus* sp. for *S. manipurensis* (Clausen 1928), and *Camponotus aethiops* (Latr.) for *S. cyniformis* (Parker 1932, 1937).

The discovery of populations of *O. floridana* and *P. gibbosa* allowed us to gather information on the oviposition habits and life histories of these species. It also provides an opportunity to make comparisons between the New World genera and the pro-

posed outgroup genus, *Stilbula,* and to reflect upon the phylogenetic relationships of these taxa.

Obeza floridana (Ashmead)
(Figs. 2, 4, 8)

Location and habitat.—The collection site was located just outside of the Apalachicola National Forest, 3.0 kilometres south of Sopchoppy, Wakulla Co., Florida. The host plant was located within a narrow windrow of *Pinus* sp. that paralleled the highway and bordered a large tree-less bog. Within the windrow, the sandy soil was covered by a thick mat of pine litter and scrub vegetation that consisted of sporadic clumps of *Cyanococcus simulatus* Small. (Ericaceae), *Diaspyros* sp. (Sapotaceae), *Cyrilla racemiflora* L. (Anacardiaceae) and *Sabal glabra* (Mill.) Sarg. (Palmae).

General observations and collections.—Collections of adult *O. floridana, Cyanococcus* fruits, and ants were made on two separate occasions in 1987—25–26 May and 4–5 June. Adult *O. floridana* were localized in their distribution and although some males were collected in a broader area, most males and all of the females except one were collected from one isolated *C. simulatus* bush. All but one of the females were devoid of eggs. Most adults were collected 4–5 June while no females and only two males were collected 25–26 May after a similar collecting effort. No copulating pairs were observed.

Cyanococcus simulatus fruits were collected and returned to the laboratory. Egg masses were maintained at 75% RH over a saturated salt solution, either within intact berries or isolated in cotton stoppered glass vials, for a one month period. Although they remained viable over this period, no hatch of mature planidia occurred. Eggs retained for a longer period succumbed to desiccation and/or fungus.

Strays of *Camponotus abdominalis floridanus* (Buckley) were found but no association could be made. Therefore, no additional immature stages of *O. floridana* became available for study. *Obeza floridana* has been reared from the pupae of *C. abdominalis floridanus* near Gainesville, Florida (Lloyd Davis, Insects Affecting Man and Animals Research Laboratory, Gainesville, FL, personal communication).

Life history.—Adult females oviposit into developing fruits of *C. simulatus* in May and June. Adults were observed hovering around the edges of the *Cyanococcus* or settled on the fruits themselves. The single gravid female readily oviposited into green berries and later dissection showed the ovaries to contain about 3500 fully developed eggs. Egg masses in the fruits consist of small clusters of 25–180 eggs (mean = 100.9, SD = 47.3, n = 15) that are deposited in pockets within the epidermal layer of the fruit (Fig. 2). They can be seen through the skin of the fruit and are associated with a minute oviposition scar. A sample of 20 berries yielded 15 egg masses with 1–5 egg masses per fruit. The eggs were found in varying states of development within a single berry from pure white (recently deposited) to a darkened coloration owing to the mature planidium inside. These observations indicate multiple ovipositions in individual fruits by different females.

No information is available on how planidia escape the fruit or enter the host ant nest. Adults of *Camponotus femoratus* Fabr. are known to collect independently the pulp and seeds of berries from a number of plants (Davidson 1988). The berries may be direct attractants to the host with planidia collected along with the fruit pulp. Deposition of eggs into a perishable fruit, as early as June, indicate that planidia complete development within the season, even though egg hatch could not be stimulated in the laboratory.

Description of the immatures.—Egg (Fig. 4): Undeveloped eggs white with a smooth chorion. Length of egg body about 0.13 mm (SD = 0.01, n = 10); of caudal stalk 0.15 mm (SD = 0.02). Mature eggs with well-

sclerotized first-instar larva occupying almost entire egg body; head oriented toward stalk and small yellowish yolk mass attached to abdominal apex (Fig. 4). Except for the more rounded appearance of the egg body, the egg is similar to those of other Eucharitidae as described in Heraty and Darling (1984).

First instar (as dissected from egg; Figs. 8, 10, 12): As described for other Eucharitinae (Heraty and Darling 1984) but distinguished as follows. Length 0.14 mm (SD = 0.01, n = 10); maximum width 0.06 mm, widest medially and circular in cross-section. Cranium with labial plates present, including hatchet-shaped posterior labial plate; two pairs of dorsal sensilla; large, paired, weakly sclerotized cranial processes arising dorsally from an unsclerotized region. Tergite I + II separated ventrally, fused dorsally; tergopleural line absent. Tergite I + II with two dorsal and one ventral pair of setae; lacking one pair of ventral setae along ventral margin of tergite III; ventral margins of tergites V–VI extended posteriorly as long narrow processes; posterior-ventral margins of tergites V–XI strongly scalloped.

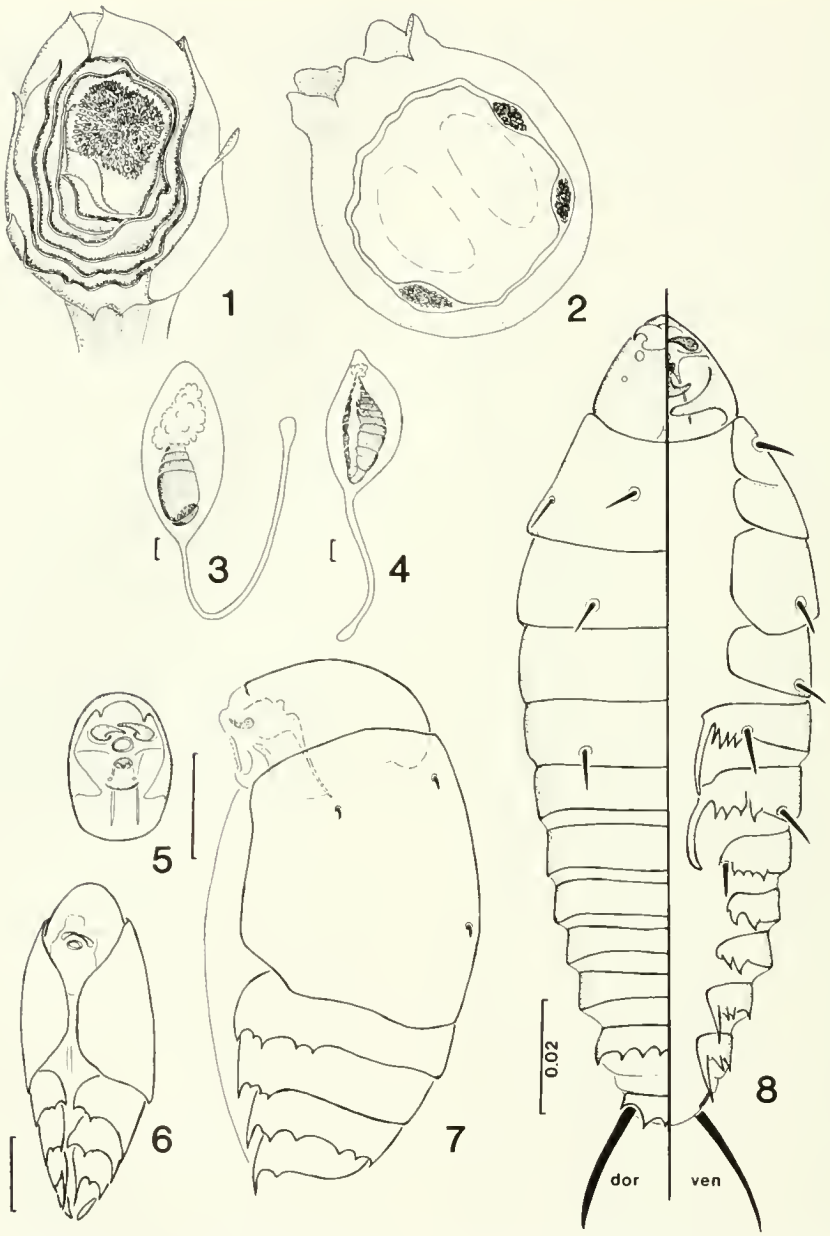
Additional information.—A second, undescribed species of *Obeza* was collected on 21 July 1987, in a dry cactus/scrub woodland habitat, 39.1 kilometres southeast of Teotitlan del Camino, Oaxaca, Mexico. Adults were observed ovipositing into the green berries of *Tragia volubilis* L. (Euphorbiaceae) which are similar in size and texture to the fruits of *C. simulatus*. The manner of egg deposition, relative size of the egg mass, and morphology of the first-instar larva were identical to those of *O. floridana*.

Pseudochalcura gibbosa (Provancher)
(Figs. 1, 3, 5–7, 9–15)

Location and habitat.—The collection site was located northeast of Sault Ste. Marie, Ontario approximately 18 kilometres northeast of Searchmont, at about mile 15 on Whitman Dam Road. The habitat is a disturbed, cutover area strewn with considerable fallen dead wood, slash, and stumps. The ground cover is predominated by *Vaccinium angustifolium* Ait., *V. myrtilloides* Michx., and *Ledum groenlandicum* Oeder. Other plants include *Polytrichum commune* Hedw. (Polytrichaceae), *Sphagnum angustifolium* (Russ.) C. Jens. (Sphagnaceae), *Gaultheria hispidula* (L.) Muhl., *Epigaea repens* L. (Ericaceae), *Cornus canadensis* L. (Cornaceae), *Clintonia borealis* (Ait.) Ras. (Convallariaceae), *Rubus* sp. (Rosaceae), and *Ribes glandulosum* Grauer. (Grossulariaceae) with scattered individuals of *Pinus strobus* L., *Abies balsamea* (L.) Mill., *Picea mariana* (Mill.) B.S.P., and *Larix laricina* (DuRoi) K. Koch (Pinaceae) and *Prunus pensylvanica* L. f. (Rosaceae).

General observations, collections, and phenology.—Adults of *P. gibbosa* were first observed 1 August 1986 as occasional males in sweep nets, in flight, or on branch tips of young spruce. No copulating pairs were observed. Female oviposition activity was localized on the floral buds of *Ledum groenlandicum* in an area of roughly 10 metres square and directed a concentration of future observations and collections here. In addition, occasional observations were made of females ovipositing in a wider area. In 1987, a Malaise trap was installed approximately 150 metres from this focus on another aspect of the edge of the cutover forest edge. Trap catches were accumulated over 7–14 day periods and those with *P. gibbosa* are summarized in Table I.

From these collections a minimum flight period of adults, particularly gravid females, occurred from 15 July to 12 August. Oviposition presumably occurs throughout this period and was supplemented by direct observation on 22 July and 11 August. The female-biased sex ratio (50:4) probably reflects differential behaviour of the sexes with concentration of activity and abundance of males in the vicinity of parasitized ant colonies where they might wait for emerging females. The lower number of spent females



Figs. 1–8. 1, Sub-sagittal section of floral bud of *Ledum groenlandicum* with single egg mass of *Pseudochalcura gibbosa*. 2, Sub-saggital section of fruit of *Cyanococcus simulatus* with three egg masses of *Obeza floridana* in different stages of development. 3. Egg of *P. gibbosa*. 4, Egg of *O. floridana*. 5–7, Planidium of *P. gibbosa*: 5, Ventral view of head; 6, Ventral habitus; 7, Lateral habitus. 8, Planidium of *O. floridana* (dor = dorsal, ven = ventral). All scale bars 0.02 mm.

Table 1. Occurrence of adult *P. gibbosa* in a Malaise trap, 1987.

Trapping Period	Days	Females		Males
		Gravid	Spent	
7–15.vii	9	1	0	0
16–22.vii	7	5	2	0
23–30.vii	8	15	7	2
31.vii–11.viii	12	4	2	2
12–25.viii	14	8	6	0
Totals	50	33	17	4

relative to gravid females (17:33) is likely due to reduced vigour and probability of flight interception after oviposition. Several *Ledum* buds were observed to have a dead spent female with its ovipositor still embedded.

Ledum buds were collected in August of 1986 and 1987 in order to obtain eggs and to attempt rearings of planidia. Eggs were held under a variety of conditions including cold storage at 2°C for four months, but even though the masses darkened relatively quickly after initial deposition (larvae matured internally), the eggs never hatched. A small sample of egg masses adhering to the dehiscing bracts of blooming *Ledum* on 29 May 1987 also failed to hatch.

Eight separate sample collections were made of *Camponotus* colonies (larvae, pupae, and adults) from 24 June to 22 July 1987. Two colonies of *C. novaeboracensis* about 20 metres from the *P. gibbosa* oviposition focus were found on 24 June not to be parasitized by *P. gibbosa*. The six collections of *C. herculeanus* (L.), on the other hand, were made within 3–5 metres of the focus. In total, four of these were eventually found to be parasitized. Ant larvae with planidia were evident in collections made on 24 June and 15 July while late-pupal or preadult *P. gibbosa* were found on 22 July.

Life history.—Adult females oviposit into the floral buds of *Ledum groenlandicum* (Ericaceae) in July and August. The ovipositor is used to penetrate directly through the bracts on the apical half of the buds. Some females are known to maintain this position on the bud for over one hour while others are found dead and devoid of eggs. These buds enclose an undeveloped inflorescence which overwinters and blooms in May–June the following season. Small, darkened, rose-brown spots visible on the external surface of the bracts could represent ovipositional scars but this was not evaluated.

Eggs are laid in the extrafloral cavities of the bud and not within plant tissue per se. One to five masses were found near the centre of the bud (not necessarily from the same female as evidenced by differential development) under several layers of bracts. The caudal stalks of the eggs were all joined at the centre of the egg mass by the apical swelling. The number of eggs in a single mass ranged from 400–1800 eggs with a mean of 943 (SD = 442, n = 10). Dissection of ovaries in unemerged females of *P. gibbosa* yielded 2000–2500 fully developed eggs. These relatively large egg masses suggest that no more than two or three ovipositions are made per female on average. It is possible that only a single oviposition is modal and some of the smaller egg masses may have been the result of interrupted oviposition during collection.

Eggs overwinter within the overwintering floral buds of *Ledum* and become exposed the following spring as the inflorescences expand. The failure of spring-collected eggs to hatch may have been because they were already dead, representing those egg masses left after dispersal of the successful planidia. The overwintering of eggs is well documented for *S. tenuicornis*. Clausen (1923) presented several ideas, which can be equally applied to *P. gibbosa*, on how the planidia eventually gain access to the *Camponotus* nest. Larvae dissected from the eggs of *P. gibbosa* after four months cold storage were viable and capable of limited (voluntary) movement of the head region. If representative of the condition of a normally eclosed

planidium, then this sharply contrasts with other members of the Eucharitidae whose planidia must actively search for their respective hosts. The means by which *P. gibbosa* enters the nest of *C. herculeanus* is unknown.

In June 1988, buds of *Ledum groenlandicum* were collected that were swollen to the point that egg masses could be observed protruding between the bracts. Egg hatch was observed shortly thereafter and the ruptured eggs produced copious amounts of liquid. The planidia were observed to undulate through the liquid and were able to occasionally lift the anterior region of the body. *Camponotus* adults were confined with the hatched egg masses and were observed to palpate the liquid mass resulting in the transfer of several larvae to the mouthparts of the ant. In one case, dead mosquitoes were also provided and the following day, macerated tissue was found with several active planidia attached. It is postulated that the egg fluid liberated by the hatch of the first instar serves to attract foraging ants which results in the transfer of several larvae to the ant. Further foraging for food or eventual tending of ant brood likely results in the transfer of several planidia to the host larva, possibly along with a food bolus. This method appears more likely than the transfer of an entire egg mass as suggested for *S. manipurensis* which should result in a tremendous number of planidia within a single colony (Clausen 1928).

In colonies of ants that were parasitized, mature larvae had an average of 3.35 planidia (SD = 1.56, n = 20). This sample represented a total of 67 planidia primarily concentrated along the creases between segments II–IV (Fig. 9). Planidia remain attached externally to the ant larva and do not burrow into the cuticle as observed for some eucharitids. They did not show any signs of feeding (as expansion of body segments) while on the ant larva until the cocoon was formed and pupation of the host initiated (Fig. 10). Clausen (1923) believed that it may be the early stages of hystolysis that trigger development of the eucharitid. Engorged first-instar larvae (Fig. 12) were found attached to the exuvium of an ant pupa within the cocoon and are presumed to be initially "cast off" and then either the first- or second-instar larvae migrate to the ventral midsection of the ant pupa (Fig. 11) where they resume feeding. No first-instar larvae were found feeding on the ant pupa. In *S. tenuicornis*, the engorged first-instar larvae were shed in a similar manner and Clausen (1923) reported that larvae moulted to a second instar before assuming the new position.

The second-instar larva was found attached to the posterior ventral portion of the thoracic region on the host pupae (Fig. 11) while the feeding position of the third instar was usually shifted dorsolaterally to the pleural region of the host. A maximum of four second-instar larvae were observed feeding on one host pupa, and as many as four pupae were found in a single cocoon although one or two were more common. Wheeler (1907) also found one cocoon with four pupae.

One engorged first instar was seen feeding upon a second-instar of *P. gibbosa*. Remains of second- or third-instar eucharitid larvae were found in some cocoons along with mature pupae of *P. gibbosa*. This suggests a cannibalistic mechanism of limiting superparasitism although the mean number of planidia per host (3.35) would generally not suggest this.

The psithergate pupae of the ants were not as strongly deformed as found in some ants attacked by eucharitids (Wheeler 1907), but did show some fusion and enlargement of the thoracic segments and poor definition of the leg segments (Fig. 11). Especially where only one *P. gibbosa* was found in a cocoon, remains of the ant host were not always devoured and one callow adult exhibited a strong resemblance to a deformed psithergate.

Description of the immatures.—Egg (Fig.

3): Undeveloped eggs white with smooth chorion. Mean length of egg body 0.17 mm (SD = 0.01, n = 10); of caudal stalk 0.24 mm (SD = 0.02). Mature eggs with well-sclerotized (black) planidial larva occupying less than half of overall volume with head oriented toward stalk; yellowish yolk mass attached to abdominal apex, filling other half of egg body.

The small size of the planidium with regard to the size of the egg body and large yolk mass may be adaptations to maintaining energy stores for an overwintering egg or act as an attractant to the ant host with the simultaneous emergence of an egg mass in the spring. A similar difference in size was not found in either *S. tenuicornis* or *S. cyniformis* which were both suspected to overwinter in the egg stage (Clausen 1923, Parker 1937).

First instar (Figs. 5–7, 12): Mean length of planidial stage, 0.08 mm (SD = 0.06, n = 10), maximum width 0.05 mm; laterally compressed, oval in cross section. Cranial sensilla absent; hatchet-shaped posterior labial plate (found in all other Eucharitinae) either absent or reduced to a barely discernible sclerite below anterior labial sclerite; pleurostomal spines and circular labial sclerite present. Reduction in number of tergites to five (Fig. 7) (12 in other Eucharitidae); tergopleural line absent. Tergites II–V (numbering not indicative of homology with same tergites in other Eucharitidae) scalloped along posterior ventral margin; strong ventral extensions of terga absent. Tergite I with three pairs of setae; all other tergal setae and enlarged caudal setae absent. The morphology of the first-instar larva of *P. gibbosa* is markedly different from any other described eucharitid.

Second instar (Figs. 11, 13): More typically hymenopteriform, white, very weakly sclerotized, with a single pair of mesothoracic spiracles (propneustic). First-instar exuvium remaining attached to ventral surface (Fig. 13). Head region weakly delineated; containing a pair of small, pincer-like mandibles. This stage is virtually identical to that of *S. cynipiformis* Rossi (Parker 1932) and *Kapala terminalis* Ashmead (as figured in Clausen 1940a) which is the only other described second instar within the Eucharitinae. *Kapala* is distantly related indicating a general conservatism of morphology in the second instar.

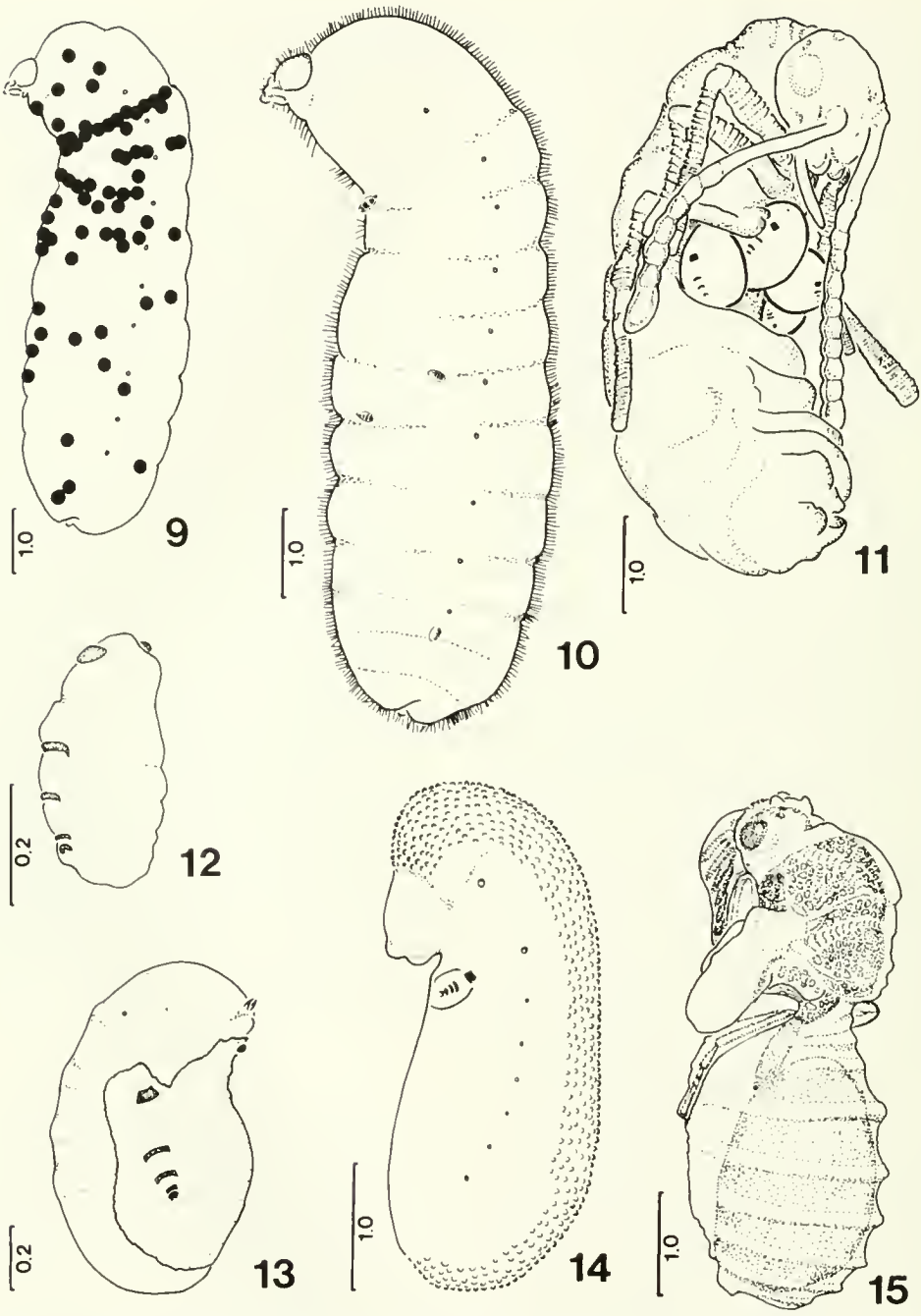
Third instar (Fig. 14): White and poorly sclerotized. Two thoracic and eight abdominal sclerites present; entire dorsal surface minutely tuberculate. Head region defined but well-developed mandibles not observed. Exuvium of first instar remaining attached to ventral thoracic region. The morphology of the third instar is identical with *S. cyniformis* (Parker 1932) and *S. tenuicornis* (Clausen 1923, 1940a).

Pupa (Fig. 15): Typically chalcid-like with exception of series of raised ridges along metasomal tergites in common with other Eucharitidae.

Additional information.—oviposition habits of *P. gibbosa* have been observed by Dr. K. Hagen (University of California, Berkeley, CA) at Amador Pines and Pioneer, Amador Co., California. Females were observed oviposited into overwintering leaf buds of *Arbutus menziesi* Pursh. in a manner which is identical to that described above. The morphology of the first-instar larva was identical with the larvae taken from Ontario.

Discussion

Obeza is the first member of the subfamily Eucharitinae which has been recorded to oviposit into fruit and have the egg chamber formed completely within the epidermal layer of the fruit as the egg mass expands during oviposition. In most other Eucharitinae, females deposit their eggs into existing cavities in plant tissue such as between the scales of an overwintering flower bud by *S. manipurensis* and *S. tenuicornis* (Clausen 1923, 1928) or into flower heads of *Picris* among the bracts or achenes as in *S. cyniformis* (Parker 1937). In contrast



Figs. 9–15. *Pseudochalcura gibbosa*: 9, Cumulative distribution of planidia on 20 mature ant larvae; 10, Early feeding stages of planidia on ant host in preparation for pupation (cocoon removed); 11, Second instars feeding on ant pupa; 12, Engorged first instar; 13, Second instar; 14, Third instar; 15, Pupa of male. Scale bars in mm.

to both *Stilbula* and *Pseudochalcura*. *O. floridana* and the undescribed species from Mexico deposit relatively few eggs in each egg mass with each female undertaking many separate ovipositions. Morphologically, adults of *Obeza* are very similar to *Stilbula* and generic differentiation is based on the possession of lateral propodeal processes and posterior extension of the genae in *Obeza* (Heraty 1985). If other species of *Obeza* share similar oviposition habits, this biological distinction serves to support recognition of the two genera.

The planidium of *Obeza* shows a number of distinctive features that provide recognition at the generic level but otherwise it is fairly typical of most Eucharitinae (see Heraty and Darling 1984). The pair of large hook-like cranial processes is similar to the anterior cranial spines found in *Perilampus* of the Perilampidae (Heraty and Darling 1984). However, the processes are unsclerotized and therefore regarded as of different derivation (not homologous) from those of *Perilampus*.

The planidium of *P. gibbosa* is highly derived within the Eucharitidae. In a family where conservatism of first-instar larvae is extreme, the reduced number of terga and lateral compression of body segments are anomalous. The reduction of segmentation of this planidium would be expected to allow very limited mobility in comparison with other eucharitids including *Stilbula* and *Obeza*. In contrast to the derived condition of the planidium, life history information and morphology of the other larval stages is virtually identical to *S. tenuicornis* (the reader is referred to Clausen (1923) for a full description) and again suggests a close relationship within the lineage regardless of their very different adult morphology.

Poor descriptions for planidia of *Stilbula* render them as generally uninformative for comparison with *Obeza* or *Pseudochalcura*. However, it is notable that the tergopleural line (a desclerotized line that runs laterally across the tergites and found in some form in all other Eucharitidae) was absent in *Obeza* and *Pseudochalcura*, and not figured in any drawings of *Stilbula* planidia. Clausen (1940a) was the first author to illustrate the tergopleural line in three other genera of Eucharitinae. In that paper, he referred to the absence of a line in *S. cyniformis* as probably due to an oversight by Parker (1932) but neglected to mention the absence in his own earlier illustrations of *S. manipurensis* and *S. tenuicornis*. Heraty and Darling (1984) similarly considered the tergopleural line as a synapomorphy of the Eucharitidae. It is now apparent that the absence of a tergopleural line may be a common feature of a clade including *Stilbula*, *Obeza*, and *Pseudochalcura*. The position of this group with respect to other Eucharitidae will need to be determined to assign correct polarity to this state.

With few exceptions, the immature stages of the Eucharitidae have proven to be very conservative in the amount of morphological change and behavioural adaptation. This allows the immature stages to provide useful evidence of higher level relationships. *Stilbula* and *Obeza* share similar adult morphology but dissimilar oviposition habits; *Stilbula* and *Pseudochalcura* share similar life histories and morphology of immatures but dissimilar adult morphology. Some of the larval and ecological characters described and compared here could represent synapomorphies or ground-plan characters of the clade discussed (e.g. general similarity of morphology of larval stages including absence of tergopleural line in planidium), thus supporting the monophyly of the clade but not providing any resolution of the relationships among the four genera. In the absence of data for other taxa, particularly *Lophyrocera*, other characters appear to be autapomorphies (e.g. cranial processes, oviposition into plant tissue in *Obeza*; reduction of segmentation in planidia in *Pseudochalcura*) that furnish no insight into inter-generic relationships. Information on the within-nest biology of *Obeza*, *Lophyrocera*, and other species of *Pseudochalcura* as well as oviposition habits and ant host

selection of these taxa throughout their geographical ranges will provide invaluable in further resolving the relationships of these taxa.

The description of the life history of *P. gibbosa*, though more extensive than that of *O. floridana*, is not exhaustive. A number of key questions still remain unanswered and certain suggestions or speculations require verification. How does the planidium travel from the *Ledum* buds to the ant nest and when is this accomplished? Reader (1977) listed only flies and bees visiting *Ledum* flowers and made no mention of ants. Do the planidia discriminate between young ant larvae (maturing in the following season) and mature larvae (pupating in same year) (Sanders 1964, 1972)? If not, how do the non-feeding planidia survive if they must remain on the host for at least a full year? These are likely to be answered only with additional observation and possibly experimentation.

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FIRST RECORD OF A BAGWORM MOTH FROM HAWAII: DESCRIPTION AND INTRODUCTION OF *BRACHYCYTTARUS GRISEUS* DE JOANNIS (LEPIDOPTERA: PSYCHIDAE)

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Abstract.—Until recently no representative of the bagworm family Psychidae was known to occur in the Hawaiian Islands. The first infestation of *Brachycyttarus griseus* De Joannis was discovered during 1984 in a residential area of Haiku on Oahu. The species has since spread to several areas on Oahu and Kauai, where the larvae feed on the introduced grass, *Paspalum conjugatum* Berg. Originally described from Vietnam, *B. griseus* has also become established in Guam where it is parasitized by a tachinid fly, *Stomatomyia* species. All stages of *B. griseus* are described and illustrated and a map showing its present Hawaiian distribution is included.

Key Words: Lepidoptera, Psychidae, bagworm, introduced species, Hawaii

Until 1984 no species of the bagworm family Psychidae was known to occur in the Hawaiian Islands. In 1984 I received specimens, which I later determined as *Brachycyttarus griseus* De Joannis, from Po-Yung Lai of the Hawaii Department of Agriculture. The infestation was discovered in a residential area of Haiku (Kaneohe, see Map 1), Oahu. This site is about 15 mi [24 km] from Honolulu Harbor, the largest shipping dock in Hawaii, and about 17 mi [27 km] from Honolulu International Airport. The bagworm is now established on Oahu and has been encountered at nine different sites in or near Honolulu and Kaneohe (Map 1). The larva is known to feed on Hilo grass, *Paspalum conjugatum* Berg, another introduced species that has already interfered with the propagation of several rare endemic plants (Vitousek et al. 1987). On Guam the larva is reported to feed on *Zoysia pungens* Willd. (= *japonica* Steud.) and "mixed native grasses" (Muniappan, in litt.).

Brachycyttarus griseus was first reported from Hanoi, Vietnam (De Joannis 1929). Considering the magnitude of traffic and shipping from Vietnam, particularly within the previous two decades, it is likely that fertile females or eggs were introduced into Honolulu during that period. However, little is known about the present species distribution. From adults examined in the Smithsonian Institution (USNM), it is apparent that *B. griseus* has existed in the Philippines for some time. Several specimens were collected at Los Baños, Luzon, some as early as 1918. Labels indicate that a few specimens were reared from grass, thus agreeing with all other host records of *B. griseus*. Also present in the same collection is a series of grass-covered cases from Serdany, Malaysia that is identical to the Hawaiian material. No adults were reared from the Malaysian cases. On the basis of specimens and reports received from R. Muniappan, L. Stevens, and R. Shook of

Map. 1. Distribution of *Brachycyttarus griseus* in Oahu. Localities represented are: 1, Ewa; 2, Waipahu; 3, Pearl City; 4, Waimalu; 5, Ajea/Halawa; 6, Aliamanu/Moanalua; 7, Salt Lake; 8, Kalihi; 9, Kaneohe.

the University of Guam, this grass-feeding bagworm was well established on Guam by 1977. Thus, the Hawaiian population could have originated from several sources, with either Vietnam or Guam perhaps the most likely.

No parasites have been reared from the Hawaiian bagworm population. Dipterous parasites reared from *B. griseus* in Guam and submitted by R. Shook have been identified by C. W. Sabrosky as Tachinidae: *Stomatomyia* species.

To facilitate the recognition of *B. griseus,* which has become more widely distributed and, thus, of greater public concern, a description of all developmental stages is provided.

Brachycyttarus griseus De Joannis
Figs. 1–48; Map 1

Brachycyttarus griseus De Joannis, 1929: 543.—Dierl, 1971: 61.

Acanthopsyche (*Brachycyttarus*) *griseus* (De Joannis).—Gaede, 1933: 735.

Adult (Figs. 1–2).—Length of forewing: ♂, 6.5–7.4 mm. A moderately small, slender, broad wing moth with uniformly dark gray wings except for short, grayish white fringe on outer margin of both wings. Apex of cucullus on male genitalia with 3 small spines. Female vermiform, naked, and without wings or segmented appendages. Larva with 6 stemmata, the most caudal 3 pairs with vestigial, flattened lenses.

Head: Vestiture sparse, gray. Mouthparts absent. Antenna 18–20 segmented, bipectinate with long slender branches; antennal sensilla long, length about 6–7× the diameter of supporting branch.

Thorax: Sparsely covered with brownish gray to gray piliform scales dorsally over dark cuticle, scales light gray to white ventrally. Forewing uniformly dark gray dorsally and ventrally with grayish white, outer fringe scales. Hindwing slightly lighter gray dorsally, mostly white ventrally; fringe grayish white. Legs with femora dark gray, tibiae and tarsi light brown to stramineous. Foreleg the longest; epiphysis long and slender, about 0.8 the length of tibia. Midleg and hindleg without tibial spurs.

Abdomen: Vestiture dark gray dorsally, grayish white ventrally; cuticle dark reddish brown to black. Eighth tergite (Fig. 41) and sternite (Fig. 42) as illustrated.

Male genitalia (Figs. 39–40): Tegumen and vinculum relatively elongate, broadly rounded. Valva approximately half the length of genitalia, divided apically into a smoothly rounded costal lobe and a smaller cucullar lobe bearing 3 short spines. Aedoeagus approximately same length as genitalia, straight, relatively stout, with caudal end slightly enlarged.

Female genitalia (Fig. 44): Anal papillae reduced to a pair of faintly setose lobes. Apophyses absent. Corpus bursae reduced to a small, digitate lobe anterior to short, broad ductus seminalis. Ductus spermathecae elongate, slender, not coiled.

Egg (Figs. 5–6).—Length approximately 0.44–0.56 mm; width 0.35–0.4 mm. Chorion smooth with stellate micropyle at one end; micropyle with 22–25 slender low ridges radiating out from central disk; arms occasionally anastomosing, forming closed cells.

Larva (Figs. 7–22, 31–38).—Length of largest larva 15 mm; maximum diameter 2.6 mm. Body color mostly white with scattered dark pigmentation over head and thoracic plates.

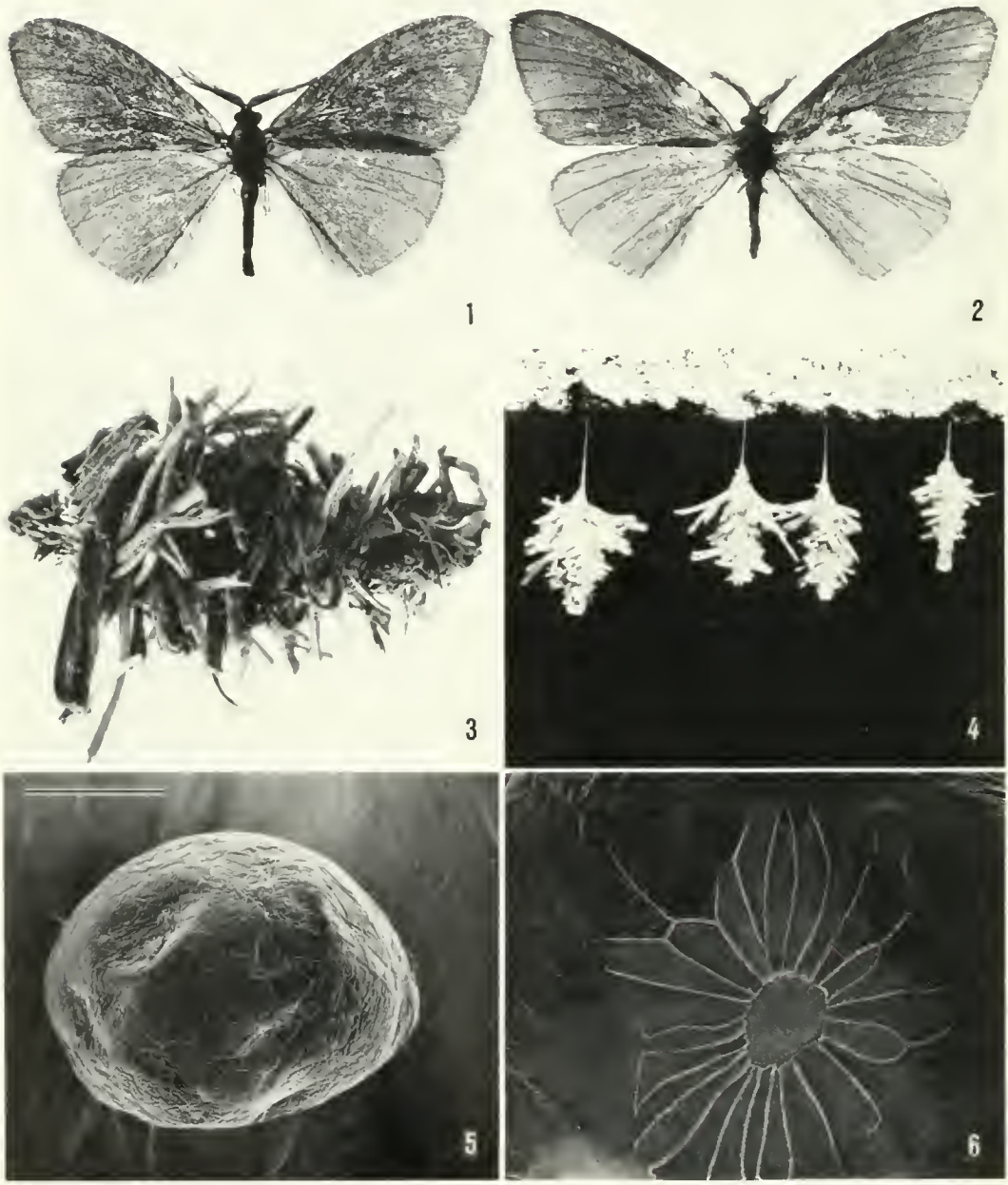
Head: Maximum width 1.5 mm. Pigmentation as in Fig. 32. AF2 elongate, extending to labrum. Six pairs of stemmata present; anterior three pairs (3–5) normal, posterior three (1–2, 6) slightly reduced with flattened corneas. S2 arising equidistant between stemmata 1 and 6 or closer to 1. Labrum with four pairs of almost equal size epipharyngeal setae. Mandible irregularly truncate; distinct cusps barely discernible. Sensilla of antenna as in Figs. 15–17; maxillary palpus as in Figs. 11–12.

Thorax: Lightly pigmented as shown in Fig. 31. Pronotum with D1 approximate to XD1. Coxal plates fused medially, with a pair of prominent lobes projecting anteriorly between coxal setae; C1 the longest. Meso- and metanotum with L2 separate from pinacula bearing L1 and 3. Tarsal claw relatively long and straight, with a small axial spine (Figs. 19–20).

Abdomen: Pinacula usually poorly defined. D1 and 2 on separate pinacula except on A8 where they arise together on a relatively large pinaculum. SD2 minute, separate from pinaculum bearing SD1 and usually slightly above and anterior to spiracle. L1 and 2 together on same pinacula on A1–2, separate on A3–9. A9 with D2 and SD1 on same pinacula. Prolegs A3–6 with 20–22 crochets in lateral penellipse; anal proleg with 15–17 crochets.

Larval case (Fig. 3).—Length 10–15 mm; diameter approximately 5–6 mm. Exterior of case densely covered with brownish grass fragments, roughly spirally arranged, thus imparting a very shaggy appearance. For pupation, case is suspended by a slender, silken strand about 0.5–1.0 the length of case (Fig. 4).

Male pupa (Figs. 23–26, 47–48).—Maximum length 6 mm; width 1.6 mm. Young pupa light brown, darkening with age until head and thorax and all appendages dark fuscous to black as well as narrow dorsal and ventral interrupted band composed of terga and sterna of A1–8. Vertex smooth, subtruncate; frontal ridge absent. Antennal



Figs. 1–6. *Brachycyttarus griseus*. 1, Male, Kaneohe, Oahu, length of forewing 6.9 mm. 2, Male holotype, Hanoi, Vietnam, length of forewing 6.6 mm. 3, Larval case, length 13 mm. 4, Larval cases, attachment for pupation. 5, Egg (176 μm). 6, Micropyle of egg (43 μm). (Scale lengths in parentheses; bar scale for Fig. 6 = Fig. 5.)

sheath extending to A3. Wing sheaths approximately same length, to middle of A3. A6–8 with a relatively short anterior row of dorsal spines as follow: A6 = 7–9 spines; A7 = 10–13; A8 = 7–10. Posterior row of dorsal spines absent. Cremaster composed of a stout pair of acute, anteriorly directed spines from venter of A10 (Figs. 25–26).

Female pupa (Figs. 27–30, 45–46).—Maximum length 7 mm; width 2.8 mm. Light brown to stramineus in color. All body appendages either absent or reduced to minute tubercules. Abdomen with both anterior and posterior dorsal spine rows reduced and present but never together on same segment; anterior row present only on A6 (= 11–14 spines) and A7 (= 10–13); posterior rows present on A1 (= 35–40), A2 (= 17–21), A3 (= 17–20), A4 (= 10–12); A5 without either anterior on posterior spine rows. Cremaster composed of a relatively slender, more reduced pair of anteriorly directed spines from venter of A10 (Figs. 29–30).

Type.—Holotype, ♂; in the Muséum National d'Histoire Naturelle, Paris.

Type locality.—Vietnam: Hanoi.

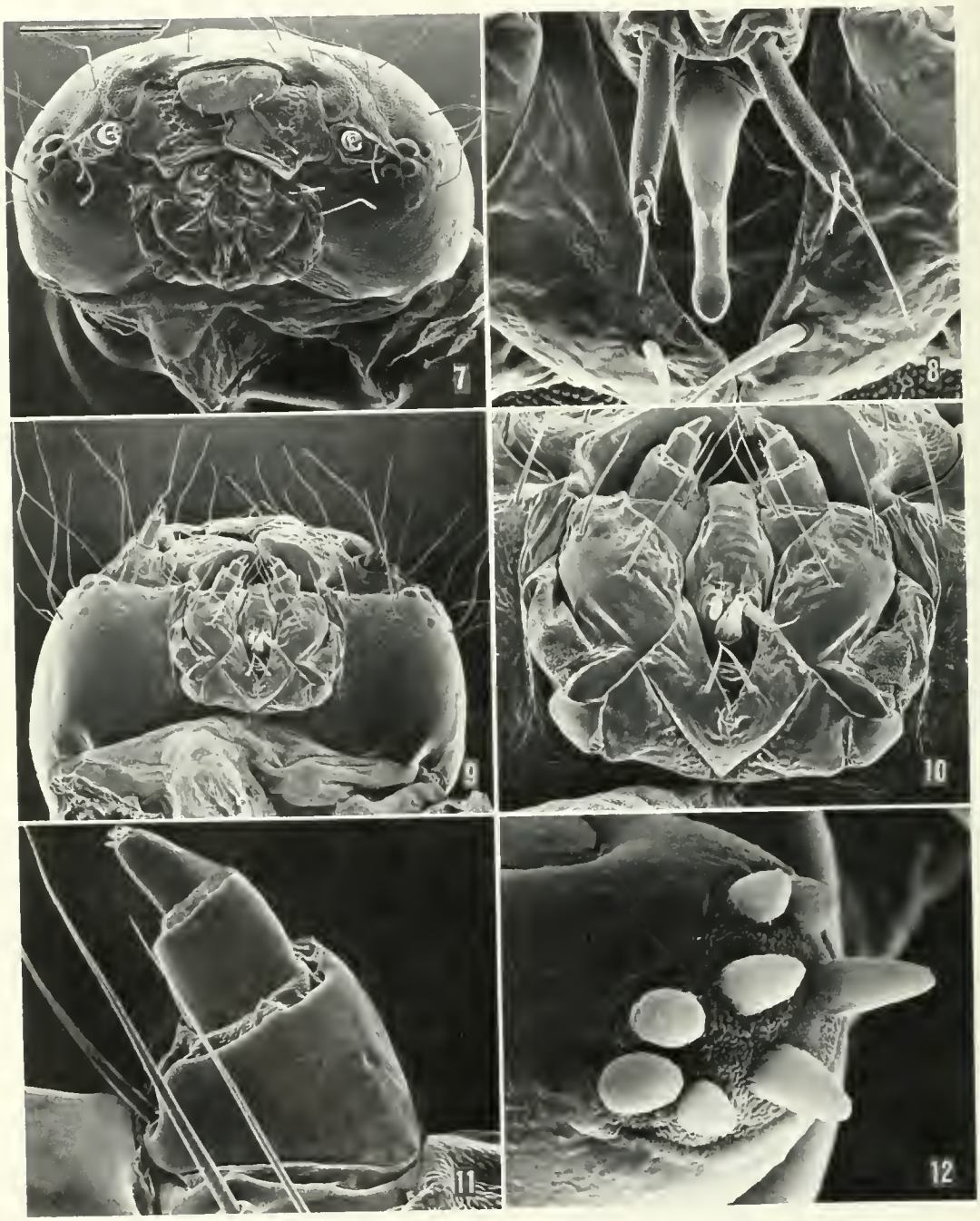
Host.—Poaceae: *Paspalum conjugatum* Berg, *Zoysia pungens* Willd. (= *japonica* Steud.) and probably other grasses.

Parasite.—Tachinidae: *Stomatomyia* species.

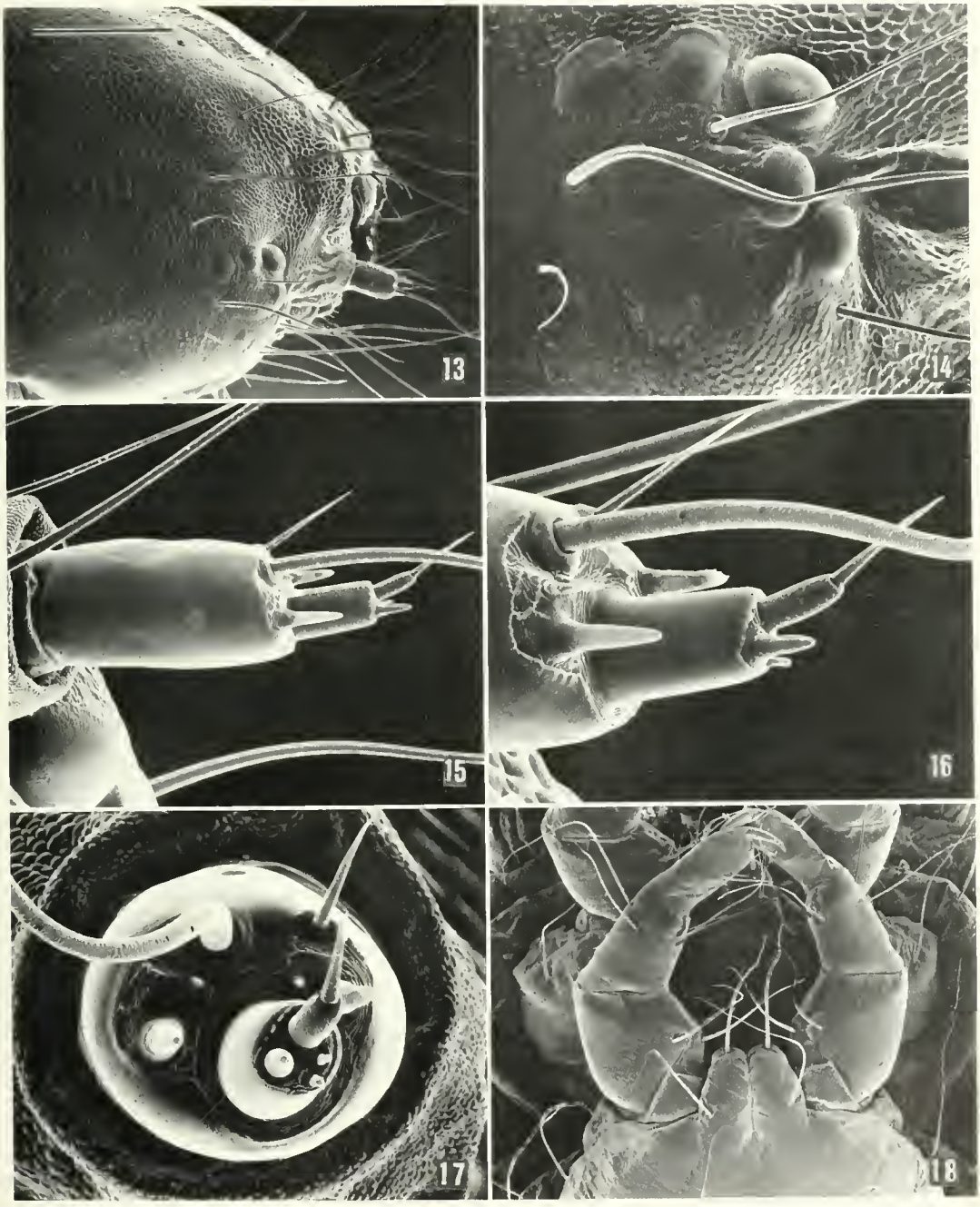
Distribution (Map 1).—Definitely known to occur in Vietnam, Philippines, Guam, and Hawaii, but probably widely distributed in southeast Asia. In Hawaii, reported only from Oahu and Kauai below 150 meters, but in time will undoubtedly spread to other major islands.

Discussion.—In his review of a few Asiatic Psychidae, Dierl (1971) treats five species of *Brachycyttarus*. Most of the species are similar in general appearance, with similar male genitalia. Consequently, species identification within this complex is difficult and still hindered by some uncertainties. Only one species, *B. fuscus* Dierl, lacks the white scales on the underside of the hindwing. Dierl illustrates the wing venation of four of the five species and indicates that both *B. griseus* and *B. fasciatus* Dierl are similar in having M2 and 3 converge at the outer margin of the hindwing (see Fig. 43). Although I have noted some venational variation in the specimens examined, the wing structure of the Hawaiian species appears closest to that illustrated for *B. fasciatus*. This is particularly evident in the stalking of R2+3 with R4+5 in the forewings and the abbreviated length of the basal radial cell in the hindwing. Lacking in Dierl's drawing of *fasciatus* is the presence of a basal stem of R that is separate from Sc as shown in Fig. 43. Partly because the male genitalia of the Hawaiian species most resemble that of *B. griseus*, I have considered them conspecific. Although the hosts of *B. fasciatus* are not stated, Dierl's comments that the larva is polyphyagous and lives only in forests under large trees and small shrubs do not suggest the species attacking grasses in Guam and Hawaii. De Joannis (1929) likewise did not state the host of *B. griseus*, but he did describe the larval case as being covered with grass fragments, which suggests grass as the foodplant. The type locality of *B. fasciatus* (Jhawani, Nepal, 200 m) also suggests a more northern species than *B. griseus*. The wing fringe of *fasciatus* was described as brown by Dierl, compared to grayish white in the Hawaiian specimens. This character has to be used with discretion, however, as only the outer fringe scales are pale colored, and these are frequently lost in rubbed specimens, as is true for the type of *B. griseus* (Fig. 2) and in most of the specimens I have examined from Guam and Hawaii.

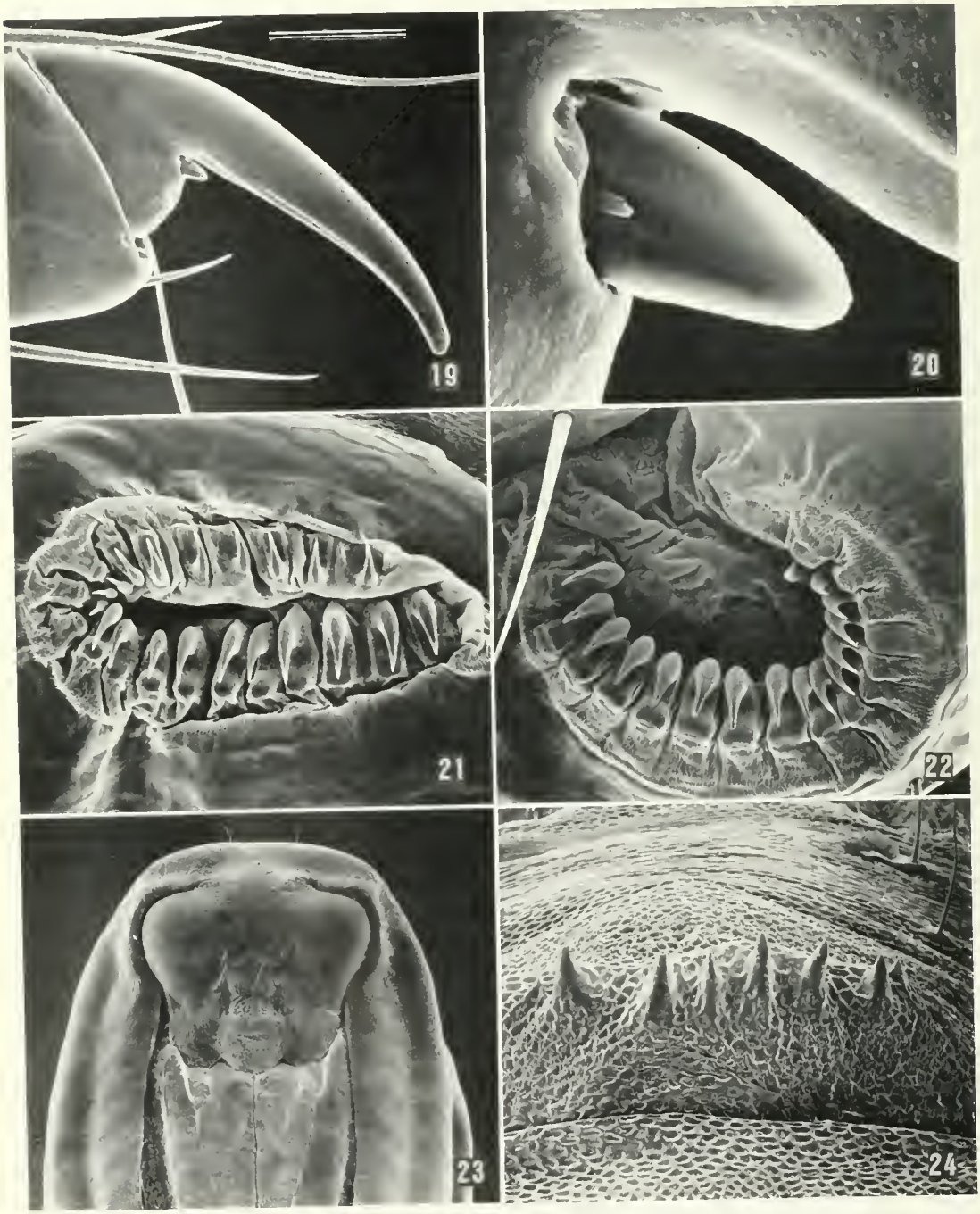
Dierl has introduced another problem in this small but troublesome genus with regard to the relatively unknown Javan species, "*Pteroma*" *reijnvaanii* Van Leeuwen. Because the original illustrations of the adult and larval case of this species most resemble *B. griseus*, *reijnvaanii* could be the senior synonym of the former. Presently this is impossible to resolve because of the in-



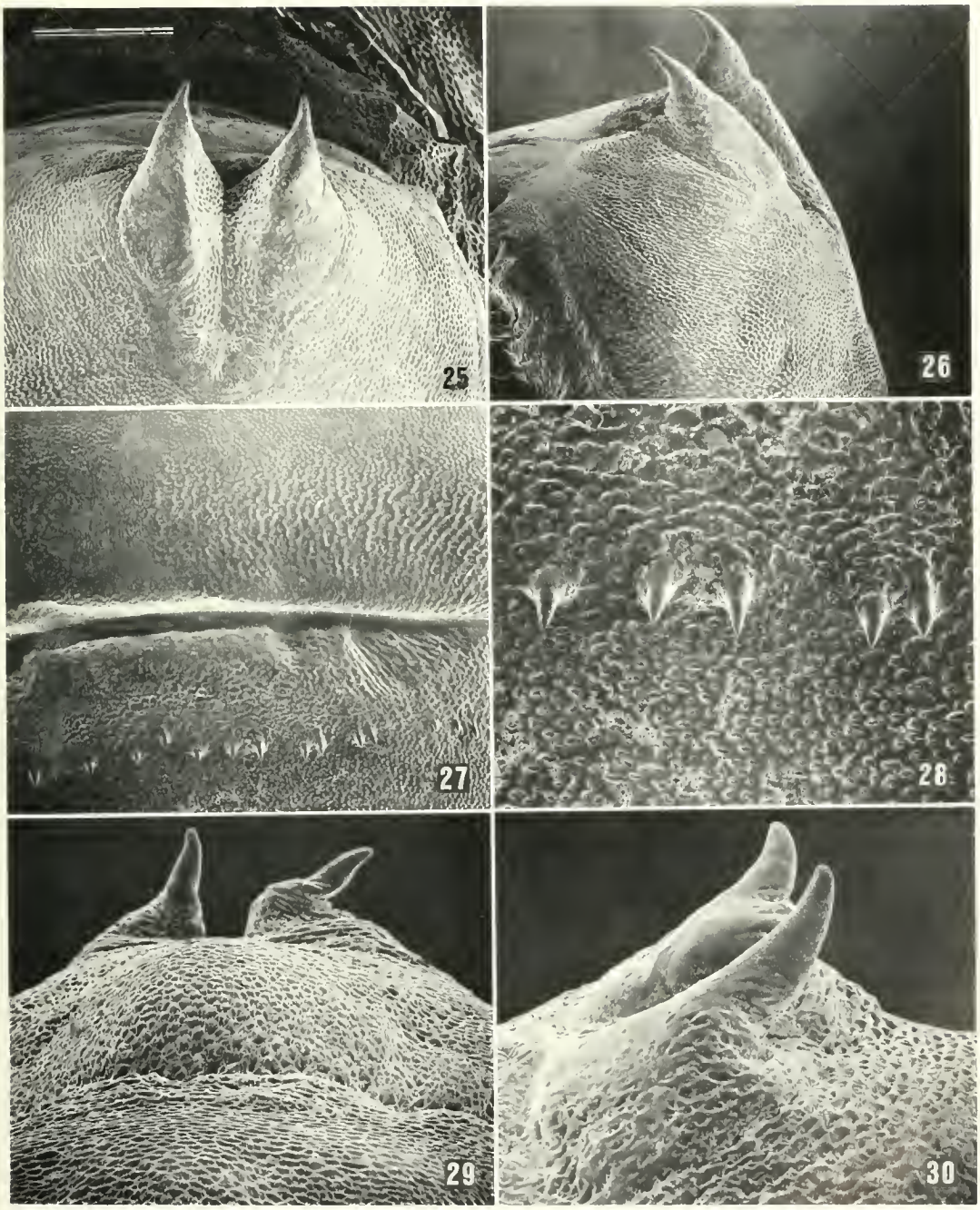
Figs. 7–12. *Brachycyttarus griseus*, larva. 7, Anterior view of head (0.43 mm). 8, Labial palpi and spinneret (60 μm). 9, Ventral view of head (0.46 mm). 10, Maxilla and labium, ventral view (200 μm). 11, Maxillary palpus (50 μm). 12, Apical sensilla basiconica of maxillary palpus (5 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 7.)



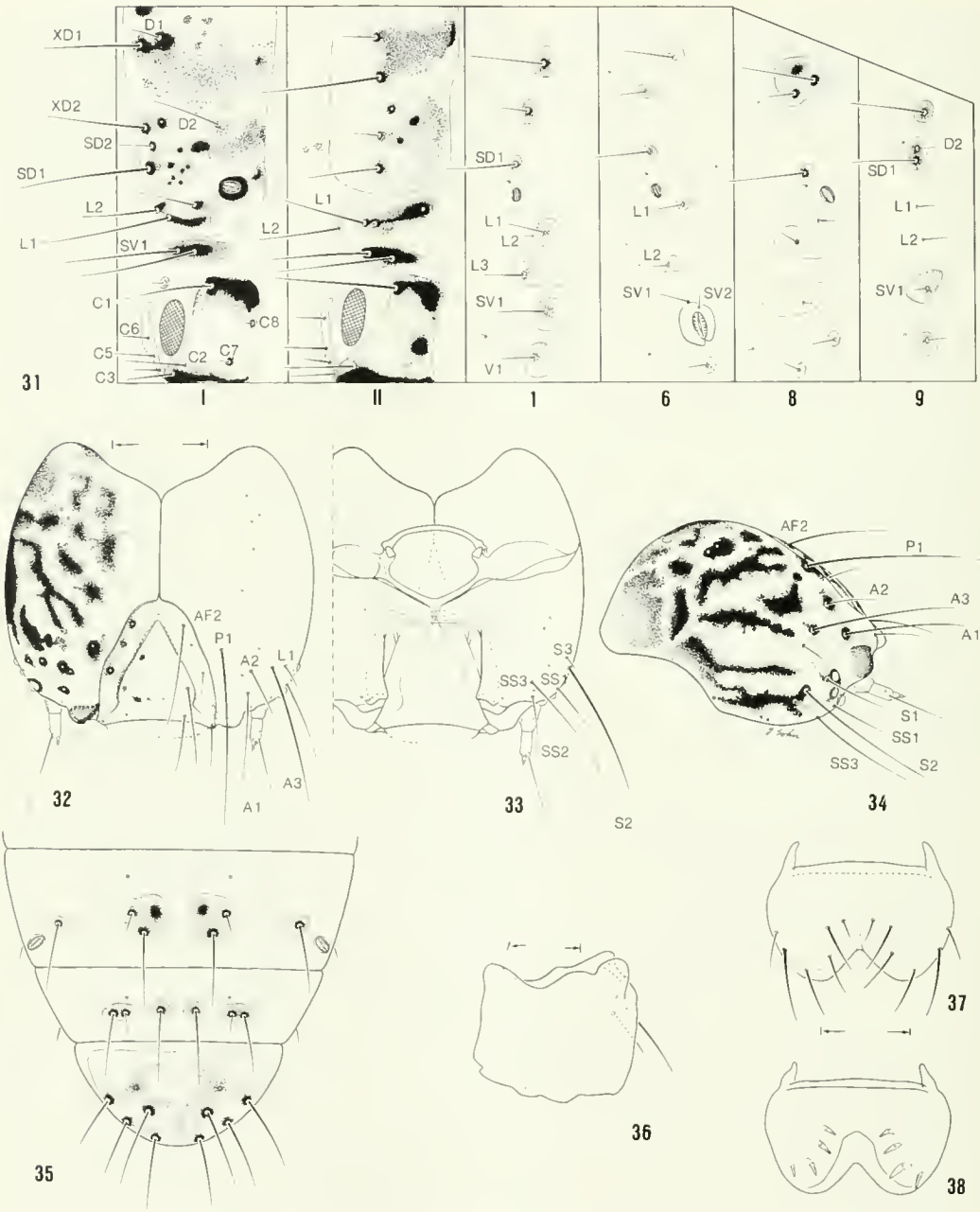
Figs. 13–18. *Brachycyttarus griseus*, larva. 13, Lateral view of head (0.3 mm). 14. Detail of stemmatal area (100 μm). 15, Antenna (60 μm). 16, Detail of Fig. 15 (30 μm). 17, Apical view of antenna (27 μm). 18, Mesothorax, ventral view (0.43 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 13.)



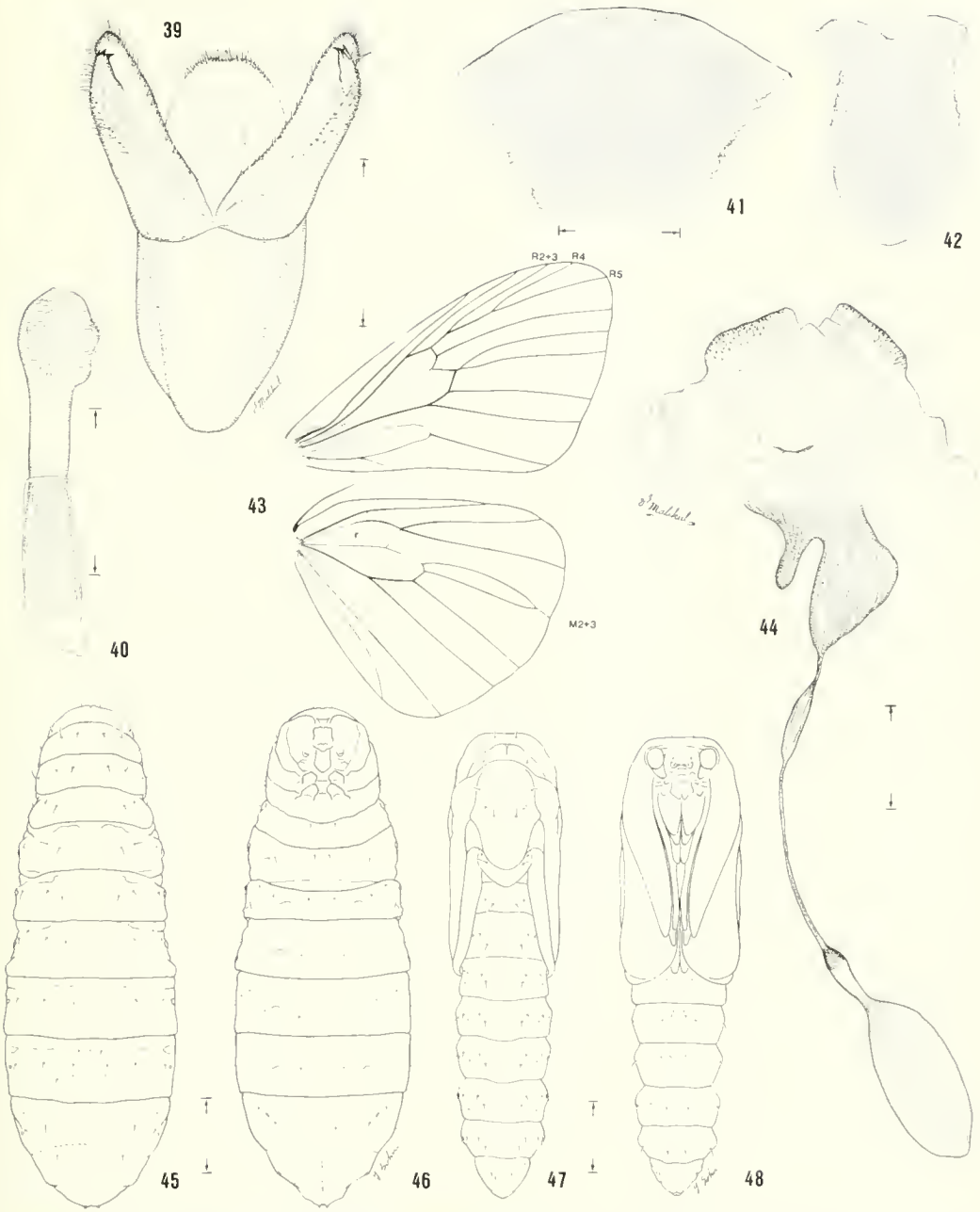
Figs. 19–24. *Brachycyttarus griseus,* larva and pupa. 19, Prothoracic tarsal claw (50 μm). 20, Detail of axial seta in Fig. 19 (5 μm). 21, Crochets of A6 (60 μm). 22, Anal crochets, A10 (60 μm). 23, Male pupa, ventral view of head (0.6 mm). 24, Male pupa, anterior row of dorsal spines A8 (86 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 19.)



Figs. 25–30. *Brachycyttarus griseus*, pupae. 25, Male cremaster, A10, caudal view (136 μm). 26, Lateral view of Fig. 25 (150 μm). 27, Female, dorsum of A6 and 7, with anterior spines on A7 (231 μm). 28, Detail of A7 spines in Fig. 27 (75 μm). 29, Female cremaster, A10, anterior view (100 μm). 30, Lateral view of Fig. 29 (60 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 25.)



Figs. 31–38. *Brachycyttarus griseus*, larval chaetotaxy. 31, Lateral view of prothorax, mesothorax, and abdominal segments 1, 6, 8, and 9. 32, Dorsal view of head (0.5 mm). 33, Ventral view. 34, Lateral view. 35, Dorsal view of A8–10. 36, Mandible (0.2 mm). 37, Labrum, dorsal view (0.2 mm). 38, Ventral view showing epipharyngeal setae. (Scale lengths in parentheses.)



Figs. 39–48. *Brachycyttarus griseus*. 39, Male genitalia, ventral view (0.25 mm). 40, Aedoeagus. 41, Tergite, A8 (0.25 mm). 42, Sternite, A8. 43, Wing venation. 44, Female genitalia (0.25 mm). 45, Female pupa, dorsal view (1.0 mm). 46, Ventral view. 47, Male pupa (1.0 mm). 48, Ventral view. (Scale lengths in parentheses.)

adequacy of the original description and the subsequent disappearance of all type material.

All eggs examined in this study, including Figs. 5 and 6, were removed from the bodies of preserved females. Consequently, their relative dimensions or even surface texture may not be typical of deposited eggs. These data eventually need to be compared with externally collected eggs for possible discrepancies.

Because this report includes the first description of the egg, larva, and pupa for any member of *Brachycyttarus*, it is not possible to compare these stages between related species. Possible diagnostic larval characters for *B. griseus* involve the elongate AF2 seta, the relative reduction of the posterior three stemmata (Fig. 14), and the reduction of the SD1 pinaculum on A9 with the consequent separation of SD2 and L1 from SD1. Comparisons involving the sensilla of the larval maxilla and antenna must await considerably more SEM work with psychid larvae. The relative amount or distribution of larval head and body pigmentation could be of some significance, although this can vary both within and between instars.

The male pupa of *B. griseus* is unusual in completely lacking the posterior row of anteriorly oriented, dorsal abdominal spines typical of most Psychidae studied (Davis 1975). The anterior row is present but only on segments A6–8. As is typical for vermiform females, the dorsal spines are greatly reduced in size in the female pupa, but their distribution is unusual. No abdominal segment possesses a full complement of both anterior and posterior rows and A5 is totally lacking in spines. Again, whether these characters are significant at the specific or generic level must await discovery of other *Brachycyttarus* pupae.

Acknowledgments

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TRIPHLEBA VITRINERVIS (MALLOCH), AN UNRECOGNIZED SPECIES OF *CRINOPHLEBA* BORGMEIER (DIPTERA: PHORIDAE)

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Abstract.—*Triphleba vitrinervis* (Malloch) belongs to the genus *Crinophleba* Borgmeier (new combination), based on a comparison with the male of *C. angustifrons* Gotô. The male terminalia are illustrated and characters are given to allow the recognition of male *Crinophleba* in the *Manual of Nearctic Diptera* key to Phoridae. *C. vitrinervis* may represent the undescribed male of *C. rostrata* Borgmeier, known only from female specimens.

Key Words: *Crinophleba, Triphleba,* Phoridae, Diptera, taxonomy

The taxonomy of phorid flies is plagued by genera described from one sex, leaving open the possibility that the male sex may be described in one genus and the female in another (e.g. Brown 1986). An example is the genus *Crinophleba* Borgmeier, described only from female specimens (Borgmeier 1967). It was compared to the genus *Anevrina,* based on the setulose Rs vein of the wing, but the female of *Crinophleba* had a much larger proboscis, shorter tergite 6, different terminalia and weaker tibial setae than *Anevrina.* No described males of North American phorids could be linked with *Crinophleba,* and it was not until a second species from Japan, *C. angustifrons* Gotô, was described from both sexes (Gotô 1983) that a male was known. The newly described male had several distinctive characters, including a narrowed frons and a lack of cerci, that were not known in any North American species of phorid. Examination of the terminalia of *T. vitrinervis,* however, showed that it was a male *Crinophleba* (NEW COMBINATION). That this was not recognized earlier is not surprising, since *C. vitrinervis* lacks the narrowed frons of *C. angustifrons* and since in the past characters of the male terminalia were not used extensively.

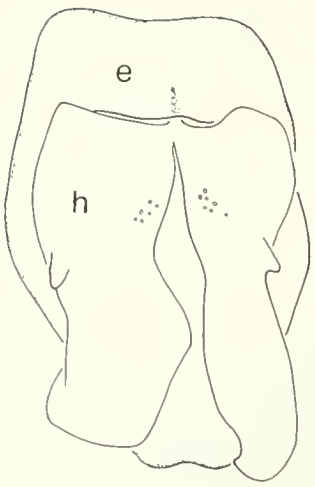
Although they have not been definitely associated, *C. rostrata* may be conspecific with *C. vitrinervis.* Definitive evidence of this relationship would be furnished by collecting the adults *in copula.* If they are conspecific, the valid name would be *C. vitrinervis.*

Below, the genus *Crinophleba* is diagnosed; the male terminalia of *C. vitrinervis* are briefly described and illustrated.

Genus *Crinophleba* Borgmeier

Type species *C. rostrata* Borgmeier (by original designation).

Diagnosis.—Frons without median furrow. Female with proboscis elongate. Anepisternum bare. Fore tibia with short, apical setae. Mid and hind tibiae with 2 anterior and 1 dorsal setae. Wing vein Rs setulose. Male terminalia lack cerci. Basiphallus expanded.



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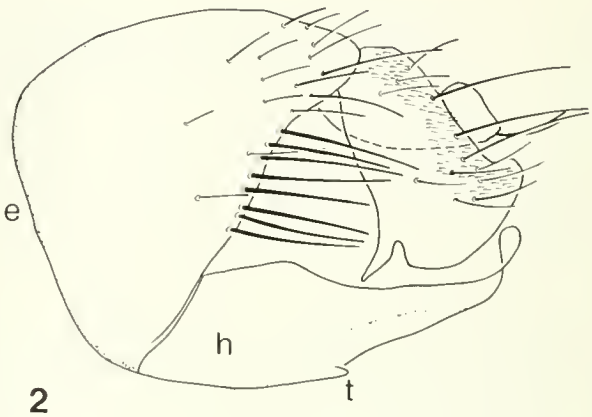

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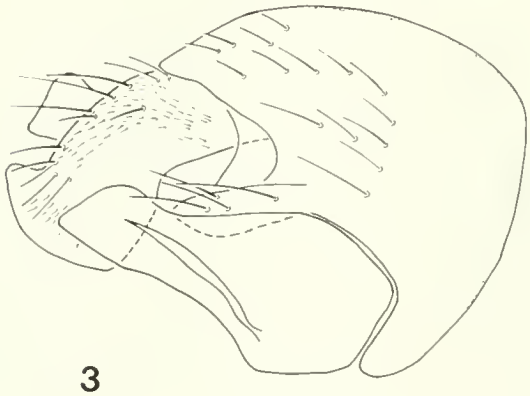

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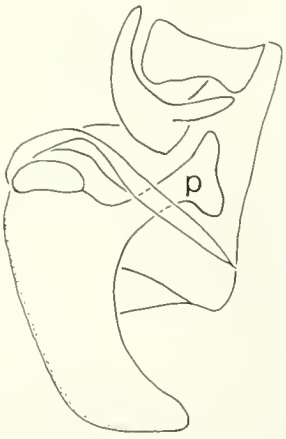

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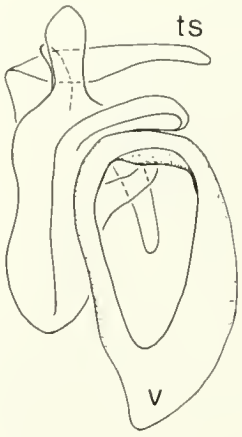

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***Crinophleba vitrinervis* (Malloch)**

Trupheoneura vitrinervis Malloch 1912: 419. *Triphleba vitrinervis*, Brues 1950: 41; Borgmeier 1963: 32.

Description.—*Male terminalia:* Epandrium continuous anteriorly, ring-shaped (Fig. 1). Left side of epandrium setose (Fig. 2); surstylus separate, with small ventral projection. Right side of epandrium (Fig. 3) setose, with posteroventral process. Hypandrium deeply cleft (Fig. 1), right lobe broader, each lobe with small lateral tooth. Basiphallus with expanded ventral portion (Fig. 5); posteriorly extended (Fig. 4). Sclerite behind basiphallus recurved above basiphallus, expanded into large lateral plate with two dorsal projections on left side and narrow lateral projection on right side. Posterior, transverse sclerite present. Cercus absent.

Material examined: CANADA. Alberta: Opal, 53°59′N, 113°13′W, 1 ♂, 20–22.vii.1989, B. V. Brown, Malaise trap, sand, jack pine. Ontario: Guelph, South Arboretum, 1 ♂, 11–16.v.1985, 1 ♂, 24–30.v.1985, 3 ♂, 19–24.vi.1985, 1 ♂, 6–10.viii.1985, Malaise trap, forest edge, 1 ♂, 7–11.vi.1985, Malaise trap, wet shrubby meadow, B. V. Brown; Stouffville, 2 ♂, 26.v.–2.vi.1985, B. V. Brown, Malaise trap (all specimens deposited in collection of the author). This species has also been collected in the states of Maryland, Michigan and New Hampshire in the U.S.A. (Borgmeier 1963).

Remarks: The wider frons of *C. vitrinervis* easily separate it from the male of *C. angustifrons*. Characters for separating female *C. rostrata* from *C. angustifrons* are given by Gotô (1983).

In order to facilitate recognition of the genus *Crinophleba* in the *Manual of Nearctic Diptera, Volume 2* key to Phoridae, couplet 8 should be changed to the following (figure numbers refer to figures in the *Manual of Nearctic Diptera*, Phoridae chapter):

8. Male lacking cerci. Female with proboscis greatly elongated, rigid (Fig. 4). Arista subapical. Scutellum with two strong posterior bristles and two much shorter coarse setae anteriorly. Tergite 6 of female short. Tibial bristles weak . . . . . *Crinophleba* Borgmeier 2 spp.; widespread in Canada and northern U.S.A.
Male with cerci present. Proboscis short, broad. Arista clearly dorsal (Fig. 35). Scutellum with four subequal bristles. Tergite 6 of female elongate. Tibial bristles strong (Fig. 65) . . . . . *Anevrina* Lioy 9 spp.; widespread in Canada and U.S.A.

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Figs. 1–5. *Crinophleba vitrinervis*. Figs. 1–3, male terminalia (bar = 0.1 mm, all figs. to same scale). 1, ventral view. 2, left lateral view. 3, right lateral view. Figs. 4–5, aedeagus (bar = 0.1 mm, both figs. to same scale). 4, left lateral. 5, frontal. ABBREVIATIONS: e—epandrium, h—hypandrium, p—posterior extension of basiphallus, t—hypandrial tooth, ts—transverse sclerite, v—ventral expansion of basiphallus.

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DESCRIPTIONS OF THE FEMALES OF THREE *POLYCENTROPUS* SPECIES (TRICHOPTERA: POLYCENTROPODIDAE)

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Abstract.—The females of *Polycentropus blicklei* Ross and Yamamoto and *Polycentropus carlsoni* Morse are described and illustrated for the first time, and the female of *Polycentropus maculatus* Banks is redescribed and illustrated. Diagnoses are provided to distinguish these females both from each other and from those of other *Polycentropus* species in the *confusus* group. Some additional life-history information for *P. carlsoni* males is provided.

Key Words: Trichoptera, Polycentropodidae, *Polycentropus*, females, descriptions

The *confusus* group is one of five New World species groups within the genus *Polycentropus*, and contains fourteen named and one unnamed species (Hamilton 1986). The need for more associations of both females and larvae with the described males of the *confusus* group was stressed by Hamilton (1986), who reviewed but did not revise the group. To date, the females of eight species have been described, and larvae have been associated with but one species. The only key to females of the *confusus* group was provided by Ross (1944, pp. 63–64, couplets 21–26) for the females of seven species, one of which was not associated with males and was referred to as *Polycentropus* species a. The female of one other species, *Polycentropus neiswanderi* Ross, has been described in the intervening years (Ross 1947).

Polycentropus blicklei Ross and Yamamoto, *Polycentropus carlsoni* Morse, and *Polycentropus maculatus* Banks are all members of the *confusus* group. Both *P. blicklei* and *P. maculatus* have been reported from several states in the eastern United States as well as from provinces in eastern Canada (Hamilton 1986), while *P. carlsoni* has been reported from only three first to second order streams in the upper Piedmont of South Carolina and lower Valley and Ridge of Alabama (Morse 1971, Lago and Harris 1987). Of these three species, only the female of *P. maculatus* has been described (Ross 1944). The efforts to discover females of *P. blicklei* and *P. carlsoni* were in response to a preliminary review considering *P. carlsoni* for possible protection under the United States Endangered Species Act of 1973, as amended. The present paper describes the females of both *P. blicklei* and *P. carlsoni* for the first time, redescribes the female of *P. maculatus*, and provides additional life-history information on males of *P. carlsoni*.

MATERIALS AND METHODS

The associations of females with males of *P. blicklei* and *P. carlsoni* were accomplished in two steps. First, intensive collection efforts for adults were made during 1988 and early 1989 using Malaise traps at and near the type locality of *P. carlsoni*. Malaise traps similar to those described by Townes (1972) were deployed from April 1988 to

February 1989 at the type locality on Wildcat Creek (site 2, see below) and on four other nearby streams within the Clemson University Experimental Forest surrounding Lake Issaqueena, Pickens County, South Carolina. Trap collections were examined weekly until the end of August, biweekly from September to the end of November, and monthly from December 1988 to the end of February 1989. Locality data of the five sites and dates of trap operations are as follows: unnamed tributary of Indian Creek (site 1), elevation 230 m, 7 April to 27 June 1988; Wildcat Creek (site 2), elevation 235 m, 4 April 1988 to 28 February 1989; unnamed tributary #1 of Sixmile Creek (site 3), elevation 225 m, 5 April to 20 June 1988; unnamed tributary #2 of Sixmile Creek (site 4), elevation 220 m, 24 April 1988 to 28 February 1989; unnamed creek at Holly Springs Picnic Area (site 5), elevation 220 m, 5 April 1988 to 28 February 1989.

In addition, five localities on streams surrounding Lake Issaqueena were sampled during May 1988 using an Ellisco® light trap with a 15-watt ultraviolet bulb. The trap was operated for a two hour period following sunset. The five localities and dates of sampling are as follows: site 5 on 8 May, Sixmile Creek on 11 May, site 4 on 20 May, site 2 on 21 May, and an unnamed first order stream on 22 May.

The second step consisted of identifying *Polycentropus* females by using the key provided by Ross (1944) and by comparing undetermined females with those associated with males during three previous surveys in South Carolina, North Carolina, and Georgia. One of these surveys was conducted on Upper Three Runs Creek and its tributaries on the Savannah River Site, Aiken County, South Carolina; another was conducted on the Lake Jocassee catchment in Oconee County, South Carolina, and Transylvania County, North Carolina; and the third survey was conducted at Spring Creek in Crawford County, Georgia. The methodology and results of the studies at Upper Three Runs Creek and Lake Jocassee catchment have been published elsewhere (Morse et al. 1980, 1989), while only partial results of the Spring Creek study have been published (Rothschild et al. 1986, Hamilton and Holzenthal 1986). The survey at Spring Creek was conducted from April to October 1983 and consisted of a Malaise trap operated continuously and supplemented by ultraviolet light trap collections two to three times each month. A number of additional specimens housed in the Clemson University Arthropod Collection (CUAC), Department of Entomology, were also examined, most notably those collected during a previous study at the type locality of *P. carlsoni* (Carlson 1971).

Specimens were examined under a Wild® M8 stereomicroscope. Measurements were taken using an ocular micrometer calibrated at 20× and are presented as a range followed by the number of specimens measured. External structures were described from uncleared specimens examined in 80% ethanol, while internal structures were described from abdomens cleared in hot 10% potassium hydroxide and examined in glycerin. Terminology of the wings follows that presented by Hamilton (1972) and Ross et al. (1982), while that of the female genitalia follows Nielsen (1980). Because so few data have been published on *P. carlsoni*, forewing lengths and flight periods of both genders are included below. All specimens examined were preserved in 80% ethanol and deposited in the CUAC.

Results and Discussion

The males of three species in the *confusus* group were collected during the survey around Lake Issaqueena. These males were *P. blicklei*, *P. carlsoni*, and *Polycentropus confusus* Hagen. Collected females belonging to the *confusus* group keyed to either *P. confusus* or *P. maculatus* when using the key provided by Ross (1944). Females of *P. confusus* were easily distinguished using the figure in Ross (1944, fig. 257) and are not con-

sidered further. Examination of the genitalia of those females which keyed to *P. maculatus* revealed two distinct forms, both of which were different from *P. maculatus* females collected during the Lake Jocassee catchment survey. The assignment of one of these two forms to *P. blicklei* was accomplished by comparison of the genitalia with those of females previously collected with *P. blicklei* males at localities where no males of either *P. carlsoni* or *P. maculatus* were collected. The studies at Upper Three Runs Creek and Spring Creek provided such sites, and females from those localities had been previously identified tentatively as *P. blicklei* by S. W. Hamilton and one of us (JCM). Females in the remaining group of maculatus-like individuals were therefore concluded to be females of *P. carlsoni*. Females of *P. blicklei*, *P. carlsoni*, and *P. maculatus* can be distinguished from those of other species in the *confusus* group by the elongate, parallel to subparallel, internal parts of gonopods VIII (Figs. 1, 5, 9), which are visible in uncleared specimens through venter VIII.

Polycentropus blicklei Ross and Yamamoto, 1965

Figs. 1–4

Coloration (in alcohol).—Eyes purple, glazed; dorsum of head, prothorax, mesothorax, and tegulae brown with erect brown to pale yellow setae; antennae, mouthparts, remainder of thorax, and legs brown to pale yellow, femora, tibiae, and tarsi with brown setae; abdominal sclerites light brown, membrane dull white. Wing membranes and veins light brown, with scattered brown setae; forewing with s-m, m, basal fork of M, m-cu, and terminal end of P clear-white, forewing margin lacking setae in spots, appearing mottled; hind wing with s-m, basal fork of M, and m-cu clear-white.

Forewing length.—Females 5.1–8.6 mm (n = 70).

Female genitalia (Figs. 1–4).—Venter VIII with ventral plates (v.pl.) narrow, blade-like, tapering apically (Fig. 1); external parts of gonopods VIII darkly sclerotized in narrow crescent anteriorly (e.gon.VIIIb), transparent posteriorly (e.gon.VIIIa) with posterior margin triangular and rounded mesally; lateral margins comprised of portions of segment IX (IXb + IXc), darkly sclerotized to ¾ length. Internal vaginal apparatus mostly comprised of "cushion" (Fig. 3) involving internal parts of gonopods VIII (i.gon.VIII), external parts of gonopods IX (e.gon.IX), and internal portion of segment X (Xd) (Nielsen 1980). Internal parts of gonopods VIII (i.gon.VIII) dark, nearly parallel, elliptical, visible through venter VIII (Fig. 1); anterior ends oblique, extending to darkly sclerotized external part of gonopods VIII (e.gon.VIIIb) at basal third of ventral plates (Fig. 1) and to base of internal portion of segment X (Fig. 3); posterior ends acute, falling distinctly short of apices of ventral plates (Fig. 1); ventral surfaces longitudinally wrinkled. External parts of gonopods IX (e.gon.IX) weakly sclerotized, not fused with internal portion of segment X (Fig. 3). Internal portion of segment X (Xd) extending anteriad only to anterior margin of tergum IX (Nielsen 1980, fig. 22, d.IX), with sclerotized lateral plates widely separated, each with rounded transverse medial projection extending nearly to midline (Fig. 2). Anterior part of genital chamber (g.ch.a.) sclerotized, semicircular, attached by postero-dorsal membranes to antero-ventral edge of internal portion of segment X (Fig. 3, Xd); trough-like with concavity extending full length of postero-ventral surface. Processus spermathecae (p.sp.) ovoid with clear central elevation bearing opening of ductus spermathecae (op.dt.sp.) (Fig. 4), ventral and lateral margins enclosed by anterior part of genital chamber.

Diagnosis.—Females of *P. blicklei* are distinguishable externally from those of both *P. carlsoni* and *P. maculatus* by the extension of the internal parts of gonopods VIII (visible through venter VIII) only to the basal third of the ventral plates of venter VIII

and from those of *P. carlsoni* by the darkly sclerotized lateral edges of venter VIII. Internally, the short, widely separated lateral plates of the internal portion of segment X and the internal parts of gonopods VIII being as long as these plates are both diagnostic.

Notes.—Females were collected from 12 April to 8 November both at ultraviolet lights and in Malaise traps.

Material examined.—GEORGIA: Crawford County: Spring Creek, approx. 5 mi SSE of Roberta, 7–12.v.1983, 1 ♀; same data, 11.v.1983, 1 ♀; same data, 21–28.v.1983, 2 ♀; same data, 10.vi.1983, 1 ♀; same data, 11–30.vi.1983, 1 ♀; same data, 8.ix.1983, 1 ♀; same data, 20.x.1983, 3 ♀; RHODE ISLAND: Richmond, 20.vi.1971, 2 ♀; same data, 30.vi.1971, 1 ♀; SOUTH CAROLINA: Aiken County: Savannah River Plant, Upper Three Runs Creek, 12.iv.1977, 1 ♀; same data, 8.vii.1977, 1 ♀; Anderson County: Pendleton, Aldwood, 1.v.1976, 1 ♀; Pendleton, Tanglewood Spring, springbrook and disturbed site, 225 m el., 30.iv.1988; 6 ♀; same data, 9.v.1988, 5 ♀; same data, 17.vi.1987, 1 ♀; same data, 30.viii.1987, 1 ♀; same data, 3.xi.1987, 1 ♀; Oconee County: Salem, Burgess Creek, 28.ix.1969, 1 ♀; Pickens County: Clemson University Experimental Forest surrounding Lake Issaqueena, sites 1–5 and an unnamed creek, 13.iv.1968, 1 ♀; same data, 14.iv.1968, 1 ♀; same data, 17.iv.1968, 1 ♀; same data, 20.iv.1968, 3 ♀; same data, 23.iv.1968, 1 ♀; same data, 24.iv.1968, 2 ♀; same data, 24.iv.–1.v.1988, 1 ♀; same data, 26.iv.1968, 3 ♀; same data, 27.iv.1968, 1 ♀; same data, 6.v.1968, 1 ♀; same data, 8–15.v.1988, 2 ♀; same data, 9.v.1968, 1 ♀; same data, 15–22.v.1988, 1 ♀; same data, 18.v.1968, 1 ♀; same data, 21.v.1988, 2 ♀; same data, 22.v.1968, 1 ♀; same data, 22.v.1988; 2 ♀; same data, 23.v.1968, 1 ♀; same data, 27.v.1968, 1 ♀; same data, 28.v.1968, 1 ♀; same data, 30.v.1968, 1 ♀; same data, 30.v.–5.vi.1988, 1 ♀; same data, 5–12.vi.1988, 3 ♀; same data, 20–27.vi.1988, 1 ♀; same data, 2.ix.1968, 1 ♀; same data, 19.ix.1968, 1 ♀; same data, 21.ix.1968, 1 ♀; same data, 26.x.–8.xi.1988, 1 ♀; Keowee-Toxaway State Park, unnamed creek, 255 m el., 19.vi.1988, 2 ♀.

Polycentropus carlsoni Morse, 1971
Figs. 5–8

Coloration (in alcohol).—Eyes purple, glazed; dorsum of head, prothorax, mesothorax, and tegulae brown with erect brown to pale yellow setae; antennae, mouthparts, remainder of thorax, and legs brown to pale yellow, femora, tibiae, and tarsi with brown setae; abdominal sclerites light brown, membrane dull white. Wing membranes and veins light brown, with scattered brown setae; forewing with s-m, m, basal fork of M, m-cu, and terminal end of P clear-white, forewing margin lacking setae in spots, appearing mottled; hind wing with s-m, basal fork of M, and m-cu clear-white.

Forewing length.—Males 4.7–6.0 mm (n = 20), females 4.5–7.3 mm (n = 35).

Female genitalia (Figs. 5–8).—Venter VIII with ventral plates narrow, blade-like, tapering apically (Fig. 5); external parts of gonopods VIII darkly sclerotized in narrow crescent anteriorly, transparent posteriorly with posterior margin triangular and rounded mesally; lateral margins not conspicuously darkened. Internal parts of gonopods VIII dark, parallel, rectangular; anterior ends oblique, extending to darkly sclerotized part of external gonopods VIII at basal fourth of ventral plates (Fig. 5) and to basal third of internal portion of segment X (Fig. 7); posterior ends oblique, falling distinctly short of apices of ventral plates (Fig. 5); ventral surfaces longitudinally wrinkled, sometimes with groove extending entire length of surface. External parts of gonopods IX fused with internal portion of segment X (Fig. 7). Internal portion of segment X extending anteriad only slightly into segment VII, nearly solid sclerite dorsally except for inconspicuous triangular opening medially (Fig. 6), anterior margin darkly rebordered and narrowly cleft medially, posterior margin inconspicuous and notched medially.

Sclerotized anterior part of genital chamber attached by postero-dorsal membranes to antero-ventral edge of internal portion of segment X (Fig. 7). Processus spermathecae ovoid with clear central elevation bearing opening of ductus spermathecae (Fig. 8), ventral and lateral margins enclosed by anterior part of genital chamber.

Diagnosis.—Females of *P. carlsoni* are distinguished externally from those of *P. blicklei* by the extension of the internal parts of gonopods VIII to the basal fourth of the ventral plates of venter VIII and from those of *P. maculatus* by the unpigmented lateral margins of venter VIII. Internally, the following characters are diagnostic: the darkly rebordered anterior margin and narrow medial cleft of the internal portion of segment X, the extension of the internal portion of segment X to the anterior margin of tergum VIII, and (like *P. maculatus*) the extension of the internal parts of gonopods VIII only to the anterior third of the internal portion of segment X.

Notes.—Males were captured from 20 April to 26 October, while females were captured from 15 April to 8 November. All specimens examined were captured in Malaise or modified emergence traps on first to second order streams in mixed hardwood-pine forests at elevations between 215 and 245 meters. The only collections of this species at ultraviolet lights were of two males in Alabama (Lago and Harris 1987).

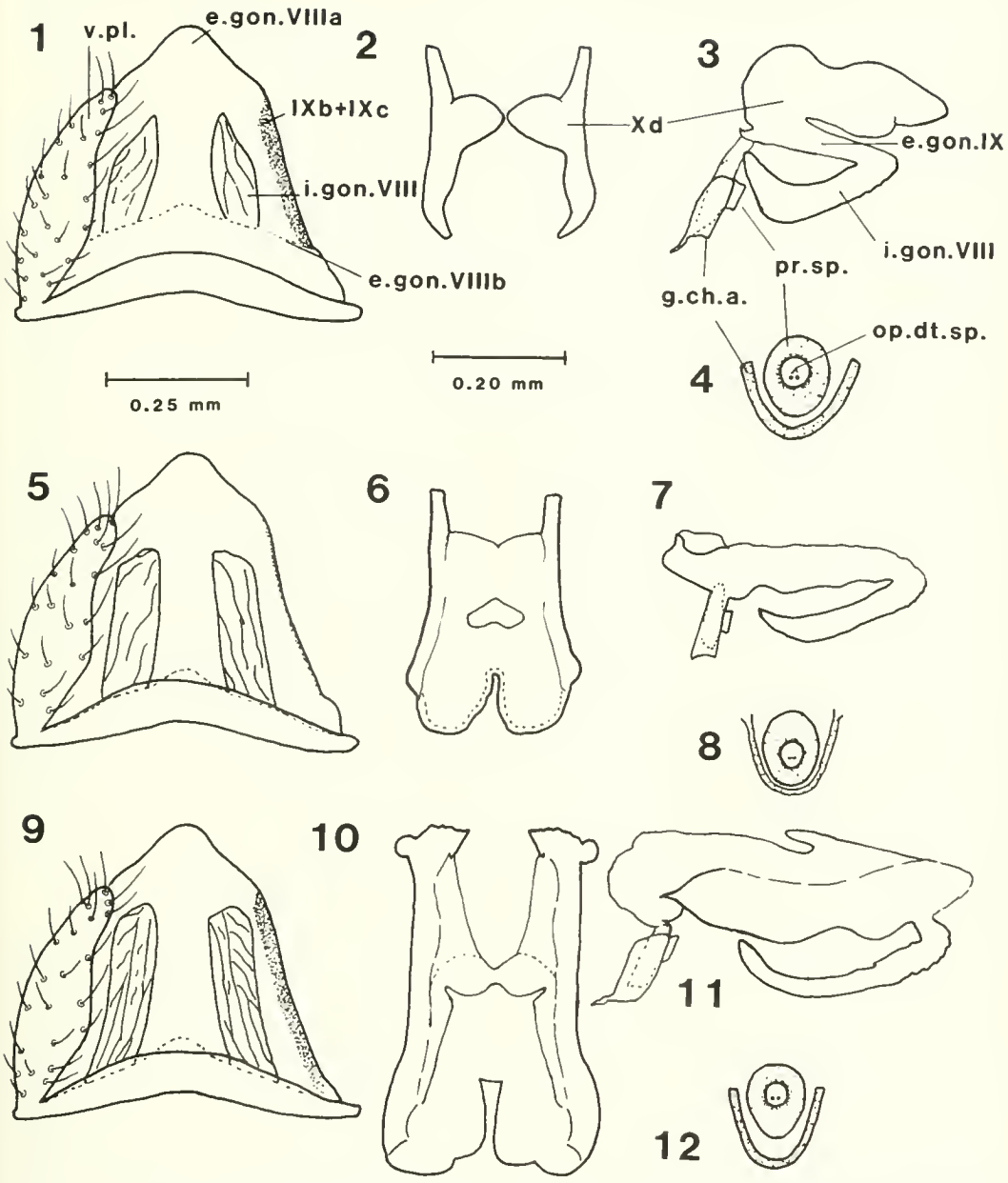
Material examined.—SOUTH CAROLINA: Anderson County: Pendleton, Tanglewood Spring, springbrook, 17–24.vi.1987, 1 ♀; same data, 15–22.vii.1987, 1 ♀; Pickens County: Clemson University Experimental Forest surrounding Lake Issaqueena, sites 1–5, 15.iv.1968, 1 ♀; same data, 20.iv.1968, 2 ♂; same data, 24.iv.1968, 1 ♀; same data, 24.iv.–1.v.1988, 1 ♂; same data, 12.v.1968, 1 ♀; same data, 15–22.v.1988, 1 ♀; same data, 22–30.v.1988, 1 ♂; same data, 30.v.–5.vi.1988, 4 ♀; same data, 5–12.vi.1988, 3 ♂ and 4 ♀; same data, 12–20.vi.1988, 6 ♂ and 2 ♀; same data, 20–27.vi.1988, 1 ♂ and 1 ♀; same data, 27.vi–4.vii.1988, 2 ♂ and 3 ♀; same data, 4–11.vii.1988, 3 ♀; same data, 11–18.vii.1988, 1 ♂ and 5 ♀; same data, 18–25.vii.1988, 1 ♀; same data, 27.vii.–1.viii.1988, 1 ♀; same data, 8–15.viii.1988, 1 ♀; same data, 15–22.viii.1988, 1 ♂; same data, 31.viii.–18.ix.1988, 1 ♂, same data, 18–26.ix.1988, 1 ♀; same data, 6–13.x.1988, 1 ♀; same data, 13–26.x.1988, 1 ♂ and 1 ♀; same data, 26.x.–8.xi.1988, 1 ♀.

Polycentropus maculatus Banks, 1908
Figs. 9–12

Coloration (in alcohol).—Eyes purple, glazed; dorsum of head, prothorax, mesothorax, and tegulae brown with erect brown to pale yellow setae; antennae, mouthparts, remainder of thorax, and legs brown to pale yellow, femora, tibiae, and tarsi with brown setae; abdominal sclerites light brown, membrane dull white. Wing membranes and veins light brown, with scattered brown setae; forewing with s-m, m, basal fork of M, m-cu, and terminal end of P clear-white, forewing margin lacking setae in spots, appearing mottled; hind wing with s-m, basal fork of M, and m-cu clear-white.

Forewing length.—Females 5.3–8.5 mm (n = 15).

Female genitalia (Figs. 9–12).—Venter VIII with ventral plates narrow, blade-like, tapering apically (Fig. 9); external parts of gonopods VIII darkly sclerotized in narrow crescent anteriorly, transparent posteriorly with posterior margin triangular and rounded mesally; lateral margins darkly sclerotized to ¾ length. Internal parts of gonopods VIII dark, subparallel, rectangular; anterior ends oblique, extending to darkly sclerotized part of external gonopods VIII at basal fourth of ventral plates (Fig. 9) and to basal third of internal portion of segment X (Fig. 11); posterior ends oblique, extending nearly to apices of ventral plates (Fig. 9); ventral surfaces longitudinally wrinkled, with groove extending entire length of surface. External parts of gonopods IX fused with



Figs. 1–12. Female genitalia of *Polycentropus* spp. *P. blicklei:* 1, venter VIII with right ventral plate removed, ventral view. 2, internal portion of segment X, dorsal view. 3, internal genitalia, left lateral view. 4, processus spermathecae and anterior part of genital chamber, caudo-ventral view. *P. carlsoni:* 5, venter VIII with right ventral plate removed, ventral view. 6, internal portion of segment X, dorsal view. 7, internal genitalia, left lateral view. 8, processus spermathecae and anterior part of genital chamber, caudo-ventral view. *P. maculatus:* 9, venter VIII with right ventral plate removed, ventral view. 10, internal portion of segment X, dorsal view. 11, internal genitalia, left lateral view. 12, processus spermathecae and anterior part of genital chamber, caudo-ventral view. v.pl. = ventral plates, e.gon.VIIIa and e.gon.VIIIb = external parts of gonopods VIII, i.gon.VIII = internal parts of gonopods VIII, IXb + IXc = portions of segment IX, e.gon.IX = external parts of gonopods IX, Xd = internal portion of segment X, g.ch.a. = anterior part of genital chamber, op.dt.sp. = opening of ductus spermathecae, pr.sp. = processus spermathecae.

internal portion of segment X and forming conspicuous twisted flange anteriorly (Figs. 10, 11). Internal portion of segment X extending anteriad halfway through segment VII and fused medially (Fig. 10), anterior margin inconspicuous and narrowly cleft medially, postero-medial margin recurved anteriorly and forming pocket. Sclerotized anterior part of genital chamber attached by postero-dorsal membranes to antero-ventral edge of internal portion of segment X (Fig. 11). Processus spermathecae ovoid with clear central elevation bearing opening of ductus spermathecae (Fig. 12), ventral and lateral margins enclosed by anterior part of genital chamber.

Diagnosis.—Females of *P. maculatus* are distinguished externally from those of *P. blicklei* by the extension of the internal parts of gonopods VIII to the basal fourth of the ventral plates of venter VIII and from those of *P. carlsoni* by the darkly pigmented lateral margins of venter VIII. Internally, the following characters are diagnostic: the deep, narrow, nonrebordered antero-medial cleft of the internal portion of segment X; the extension of the internal portion of segment X anteriorly to the middle of abdominal segment VII; the conspicuous, twisted antero-lateral flanges of the internal portion of segment X; and (like *P. carlsoni*) the extension of the internal parts of gonopods VIII only to the anterior third of the internal portion of segment X.

Notes.—Females were collected from 18 May to 15 September at ultraviolet lights and in Malaise traps.

Material examined.—GEORGIA: Union County: Vogel State Park, Wolf Creek, 22.vii.1972, 1 ♀; NORTH CAROLINA: Transylvania County: Bearcamp Creek at 420 m el., 20–21.vii.1987, 2 ♀; SOUTH CAROLINA: Oconee County: Coley Creek at 420 m el., 20–21.vii.1987, 2 ♀; same data, 14–15.ix.1987, 3 ♀; E. Fork Chattooga River, U.S. Fish Hatchery, 13.vii.1969, 2 ♀; Thompson River at NC border, ca. 420 m el., 18–19.v.1987, 1 ♀; same data, 15–16.vi.1987, 1 ♀; Pickens County: Rocky Bottom, Eastatoe Creek, 5.vii.1969, 3 ♀; Table Rock, Carrick Creek, 10.viii.1969, 1 ♀.

The similarity of the females of *P. blicklei, P. carlsoni,* and *P. maculatus* reinforces the close relationships between these species alluded to in the original descriptions of the males of both *P. blicklei* and *P. carlsoni.* Ross and Yamamoto (1965) compared and contrasted the male genitalia of *P. blicklei* with those of *P. maculatus,* and Morse (1971) stated that males of *P. carlsoni* most closely resembled those of *P. blicklei.* However, characters of the female genitalia point to a closer relationship between *P. carlsoni* and *P. maculatus* than between either of these and *P. blicklei.* The long, medially-fused internal portion of segment X; the deep, narrow antero-medial cleft of this structure; and the long rectangular internal parts of gonopods VIII appear to be homologues unique to the former two species. Thus, characters of the female genitalia may well prove useful in constructing a phylogeny for the *confusus* group and may add significantly to phylogenetic analyses of other New World species groups of *Polycentropus* as well.

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NEW SUBFAMILY PLACEMENT FOR SOME NORTH AMERICAN EULOPHIDAE (HYMENOPTERA, CHALCIDOIDEA)

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Abstract.—The tetrastichine genus *Parachrysocharis* Girault (Eulophidae), previously treated in North American literature as a member of the subfamily Entedoninae, does not occur in North America. The one North American species that was included in this genus, *P. semiflava* Girault, is transferred to the tetrastichine genus *Chaenotetrastichus* Graham. This is the first record of this genus from North America. The genus *Apterolophus* Gahan, previously placed in the Eulophinae (Elachertini), is transferred to the Tetrastichinae and synonymized with *Tetrastichomyia* Girault. *Tetrastichomyia orygiae* Girault is a junior synonym of *T. clisiocampae* (Ashmead) and *T. silvensis* is reinstated into *Tetrastichomyia* from *Tetrastichus.*

Key Words: first record, *Parachrysocharis, Apterolophus, Tetrastichomyia, Chaenotetrastichus*

In the course of independent studies in the family Eulophidae, we realized that certain North American genera have been traditionally misunderstood, either as to their proper identity, their subfamily placement, or both. This paper arose from the need to correct two such mistakes in order to facilitate the delimitation of eulophid subfamilies necessary for future work.

Genus *Chaenotetrastichus* Graham

Chaenotetrastichus Graham, 1987: 25.

Type species: Tetrastichus grangeri Erdös (original designation).

The genus *Parachrysocharis,* described in the Entedoninae by Girault (1913), recently was characterized and discussed by Boucek (1988), who transferred it to the Tetrastichinae. It presently contains only the type species, *P. javensis* Girault (1913), previously treated under the name *Tetrastichus pyrillae* Crawford, which is a parasite of *Pyrilla* eggs in southern Asia. Girault (1917) described a North American species in the genus *Parachrysocharis, P. semiflava.* This species clearly does not belong in the genus *Parachrysocharis,* which is very distinct due to the unique longitudinal striations on the mid lobe of the mesoscutum (see Boucek 1988). Girault's North American species has been treated in the Entedoninae in all catalogues since its description (Peck 1951, 1963, Burks 1979). Examination of the types of *P. semiflava* showed us that it actually belongs in the recently described tetrastichine genus *Chaenotetrastichus* Graham (1987). This genus was known previously only from Europe.

The genus *Chaenotetrastichus* was described based on a single European species, *Tetrastichus grangeri* Erdös. Diagnostic characters for the genus, given in the text and in the generic key presented in the same work (Graham 1987), are as follows: sub-

marginal vein with 1 dorsal seta; scutellum with 5–6 pairs of setae; mandible with a long, falcate outer tooth and two very small, closely approximated inner teeth; dorsal surface of thorax dull, with raised reticulation; mid lobe of mesoscutum without a median line, with 2–3 irregular rows of long, erect setae on each side; dorsal surface of gaster wholly, finely reticulate; body brightly metallic green to blue-green.

Parachrysocharis semiflava Girault belongs in the genus *Chaenotetrastichus*, although it differs in several key characters (based on *grangeri*). The scutellum only possesses 3–4 pairs of setae; the mesoscutum only has 1 row of 3–4 setae along each lateral margin (in both species the setae on the mesoscutum and scutellum are long, whitish, and semi-erect); the gaster is distinctly reticulate on the first tergum, but only faintly reticulate after that; the body is metallic green dorsally, yellow ventrally. Otherwise, it matches the diagnosis of *Chaenotetrastichus* well, particularly the peculiar mandible shape, which is unique to this genus, the single seta on the submarginal vein, and the distinct reticulation of the thorax.

Chaenotetrastichus presently contains two species:

C. grangeri (Erdös). *Tetrastichus grangeri* Erdös, 1958 (1957): 286–287. Holotype ♀, FRANCE, Chartrettes, 11.vi.1950, C. Granger.

C. semiflavus (Girault), NEW COMBINATION. *Parachrysocharis semiflava* Girault, 1917: 129. Lectotype ♀ (present designation), TEXAS, Austin, 16.viii.1909, C. Hartmann [USNM type no. 20803, examined].

The lectotype ♀ of *C. semiflavus* is mounted on a point and has been labelled as lectotype. The USNM collection also contains a female paralectotype with the same data as the lectotype and a slide on which Girault mounted a head and several pieces of a body from a third specimen. The rest of this specimen is missing.

Genus *Tetrastichomyia* Girault

Tetrastichomyia Girault, 1916a: 48.

Type species: *Miotropis clisiocampae* Ashmead, 1894 (original designation).

Apterolophus Gahan, 1919: 3–4. NEW SYNONYM.

Type species: *Apterolophus pulchricornis* Gahan (original designation).

The type species of *Apterolophus* was set through original designation, not monotypy as stated in North American catalogues (Peck 1951, 1963, Burks 1979).

Girault (1916a) described the genus *Tetrastichomyia* based on the single species *Miotropis clisiocampae* Ashmead. He later described two more species in this genus, *T. orgyiae* and *T. silvensis* (Girault 1916b). These three species were subsequently assigned to *Miotropis* Thomson by Peck (1951) when he synonymized *Tetrastichomyia* under *Miotropis* and later were transferred to *Syntomosphyrum* (Burks 1967, 1979). Graham (1987) provided a key to European genera of Tetrastichinae, in which he resurrected the genus *Tetrastichomyia*, and presented the following diagnostic characters: dorsellum divided medially by a groove or ridge; propodeum with a sharp carina on the callus, raised reticulation with rugosity or wrinkles, and a small spiracle; third anellus larger than the preceding two and setose (at least in European and North American species); scutellum without submedian lines, sublateral lines deep with lateral edge carinate; vertex with transverse ridge posterior to ocellar triangle; lower edge of antennal toruli level with ventral edge of eyes; mid lobe of mesoscutum without medial line; frons without transverse suture.

Gahan (1919) described the genus *Apterolophus* in the subfamily Elachertinae (now considered the tribe Elachertini of the Eulophinae). It has since been maintained in Eulophinae, even though at the time of its description Gahan mentioned its close sim-

ilarity to *Miotropis clisiocampae* Ashmead, which has since been transferred to the Tetrastichinae. Our studies indicate that *Apterolophus* is indeed a tetrastichine, and we are assigning it to this subfamily, where we are synonymizing it with *Tetrastichomyia*, a genus based on the species *M. clisiocampae*.

Examination of *Apterolophus pulchricornis* Gahan, the type species and only included species in the genus *Apterolophus* Gahan, shows that it agrees with all the key characters given by Graham. It differs from other species in *Tetrastichomyia* in that the female is brachypterous. The male is unknown.

At present there are three North American species placed in the genus *Tetrastichomyia*:

T. clisiocampae (Ashmead). *Miotropis clisiocampae* Ashmead, 1894: 341. Lectotype ♀ (present designation), WEST VIRGINIA, Morgantown, 28.vi.1891, A. D. Hopkins, ex. *Clisiocampe americana* on apple [USNM type no. 2183, examined]. As the type of *Tetrastichomyia*, this combination was revived through implication by Graham (1987: 28) when he resurrected the genus *Tetrastichomyia*.

T. orgyiae Girault, 1916b: 112. **New Synonym.** *Tetrastichomyia orgyiae* Girault. Holotype ♀, WASHINGTON, D.C., xi.1915, R. M. Fouts, ex. *Orgyia leucostigma* [USNM type no. 20399, examined].

T. orgyiazele Burks, 1979: 1005. **New Synonym.** Unnecessary replacement name. Burks (1979) assigned *Syntomosphyrum orgyiazele* as a replacement name for *Tetrastichomyia orgyiae* Girault (nec *Syntomosphyrum orgyiae* Ashmead) when he transferred *T. orgyiae* Girault to *Syntomosphyrum*.

T. pulchricornis (Gahan), **New Combination.** *Apterolophus pulchricornis* Gahan, 1919: 3–4. Holotype ♀, NEW YORK, Leeds, viii.1918, W. M. Mann [USNM type no. 21910, examined].

T. silvensis Girault, **Revived Combination.** *Tetrastichomyia silvensis* Girault, 1916: 111. Holotype ♀, MARYLAND, Glenndale, 16.vii.1915 [USNM type no. 20398, examined]. This species was described in 1916, in the same paper as *orgyiae*; however, the date of publication has been incorrectly given as 1919 in North American catalogues (Peck 1951, 1963, Burks 1979).

The lectotype of *clisiocampae* Ashmead is point mounted on a pin with three other specimens (paralectotypes) of the same species. The lectotype point has been marked with a black dot to indicate the proper specimen and a lectotype label has been added to the pin.

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DESCRIPTIONS OF A NEW SPECIES AND THREE INCOMPLETELY KNOWN SPECIES OF WESTERN NEARCTIC *ISOPERLA* (PLECOPTERA: PERLODIDAE)

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Abstract.—The male, female, nymph, and egg of ***Isoperla miwok***, new species, are described from a Sierra Nevada intermittent stream, California. Distinguishing features include male aedeagal shape and spination, female subgenital plate shape, adult and nymphal pigment patterns, and microstructure of the collarless egg. This new species is placed in the *Isoperla sobria* (Hagen) complex. The male aedeagus, female, nymph, and egg of *Isoperla acula* Jewett are described, and this species is moved to the *Isoperla quinquepunctata* (Banks) complex. Males have a unique patch of sclerotized scales encircling the aedeagus near the apex. Other features include the triangular subgenital plate of the female, the pigment pattern of the nymph, and the collarless egg. *Isoperla acula* is closely related to *Isoperla mormona* Banks, but differs by inhabiting small intermittent streams. Nymphs of *Isoperla adunca* Jewett and *Isoperla bifurcata* Szczytko and Stewart are described, and both species are retained in the *Isoperla sordida* Banks complex. *Isoperla adunca* nymphs are unique among western Nearctic *Isoperla* species by lacking longitudinal abdominal stripes.

Key Words: Plecoptera, Perlodidae, *Isoperla*, new species, western Nearctic species complexes

Twenty-two species of *Isoperla* are currently known from the western Nearctic region (Stark et al. 1986), and relationships within this group have been elucidated in recent revisions by Szczytko and Stewart (1979, 1984). Using morphological characters of adults, nymphs, and eggs, they erected five species complexes for 20 *Isoperla* species, and two species remained unassigned. Placement of some species within these complexes was tentative because certain life stages were unknown. Presently, one male, one female, ten nymphs, and two eggs of the 22 *Isoperla* species are unknown or incompletely described. Szczytko and Stewart (1979) have stressed the desirability of completing these life stage descriptions for a better understanding of phylogenetic relationships in this group. Further descriptions of several *Isoperla* species endemic to California are especially needed because this region is important in the group's evolution, past dispersal, and zoogeography.

During a study of stoneflies in the central Sierra Nevada of California, we collected and associated many adults and nymphs of *Isoperla*. In the process, a new species was discovered, plus the undescribed life stages of three rarely collected species were collected, *Isoperla acula* Jewett (male aedea-

gus, female adult, nymph, and egg), *Isoperla aduncа* Jewett (nymph), and *Isoperla bifurcata* Szczytko and Stewart (nymph).

The objectives of this paper were to (1) describe all life stages of a new *Isoperla* species from California, (2) complete the descriptions of all life stages of *I. acula*, *I. aduncа*, and *I. bifurcata*, and (3) relate these new data to the five *Isoperla* species complexes.

Materials and Methods

This study was based on collections of *Isoperla* nymphs and adults from many habitats in the Cosumnes River basin (sea level to 2249 m elevation) on the western slope of the central Sierra Nevada, California. Positive nymph/adult associations of all four species were made by rearing mature nymphs to emergence in the field and/or laboratory using small growth containers. Cool water temperatures (4–12°C) were necessary to maintain *I. bifurcata* nymphs until they emerged, but the other three species collected from low elevation habitats emerged successfully at much warmer water temperatures (15–29°C). Teneral adults were held in the laboratory to obtain eggs.

Adult and nymphal drawings were made with a Wild M5-A stereo dissecting microscope and camera lucida. The microstructures of nymphal mouthparts, terga, and eggs were examined using compound and scanning electron microscopes (SEM). Eggs oviposited into holding containers or dissected from preserved gravid females were prepared for SEM study as described by Szczytko and Stewart (1979), and micrographs were made with an ISI Super III SEM. Male terminalia were treated for study according to the methods of Szczytko and Stewart (1979). Aedeagal armatures were examined from temporarily mounted sections in glycerol, and were studied with a Zeiss Standard RA, Routine and Research compound microscope. To facilitate study of the males, the aedeagus of living specimens was everted just prior to preservation.

Voucher specimens of all four *Isoperla* have been deposited in the National Museum of Natural History (USNM), Washington, D.C.; California Academy of Sciences (CAS), San Francisco, Calif.; and Brigham Young University, Provo, Utah. Additional specimens are in the collections of S. W. Szczytko and R. L. Bottorff.

Results and Discussion

Isoperla miwok Bottorff and Szczytko, New Species

Male.—Macropterous. Body length 8–10 mm; forewing length 7.5–9.5 mm, slightly exceeding abdomen. General body color light to medium brown. Dorsum of head creamy yellow, dark band connecting median and lateral ocelli; interocellar area light; light spot anterior to median ocellus; occiput light brown behind lateral ocelli, with reticulations (Fig. 1). Antennae brown, pedicel and scape margins dark. Pronotum with light median stripe, disks medium brown, rugosities dark, anterior and posterior margins dark, anterolateral corners light (Fig. 1). Meso-metanota with light median stripe or spot anteriorly. Wings light brown. Femora with light-dark distal bands. Abdominal terga with two mesal longitudinal rows of dots. Vesicle absent. Paraprocts pointed, deflected outward at tips, recurved over posterior margin of tenth tergum, slightly crenulated and bearing short setae (Figs. 2, 3). Aedeagus membranous with expanded balloon-like apical section bearing 2 small rounded lobes and a long, narrow, tail-like, anteromedian tube (difficult to see and evert in preserved specimens) covered with fine rounded spinulae (Fig. 4B) and a posteromedian truncated lobe void of spinulae (Fig. 4); posteroapical patch of large, heavy, reddish brown spines (Fig. 4C); mesal area covered with stout, evenly spaced, proximally projecting, golden brown spinulae (Fig. 4A) and posterior band of large, heavy, proximally projecting, reddish brown spines which grade into smaller, lighter spines

proximally (Fig. 4D); proximal area with fine shallow scales bearing microtrichia and small fine spinulae (Fig. 4E). Cercal segments with a long posteroventral seta.

Female.—Macropterous. Body length 10–12 mm; forewing length 9–11 mm, slightly exceeding abdomen. Body color and external morphology similar to male. Subgenital plate truncate, wide at base, produced at least ½ length over 9th sternum; posterior ⅓ dark brown, posterior margin evenly rounded; scattered long fine hairs mesally (Fig. 5).

Nymph.—Body length of mature nymph 10–14 mm. General body color medium brown. Dorsum of head with a dark wide lateral band between ocelli and antennal bases, which extends anterolaterally and encloses a small light spot; interocellar area light; triangular light area anterior to median ocellus connecting to transverse light band across frontoclypeus, posterior corners of triangle extending as thin light lines to antennal bases; epicranial suture light; occiput bearing irregular row of short spinulae (Fig. 6). Lacinia triangular, bidentate; 1 axillary seta; 8–9 long marginal setae below subapical tooth (1 thin seta at tooth base, then 7–8 equally-spaced stout setae); 2 long stout submarginal setae below base of main tooth; sparse marginal and submarginal fine setae extending to lacinia base (Figs. 7, 8). Mandibles with 6 teeth, outer 3 teeth serrated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 9, 10); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 11, 12). Antennae 80–100% of body length, 60–69 segments. Pronotal median stripe, lateral margins, and rugosities light; disks brown; margins fringed with short to long setae; angles rounded (Fig. 6). Legs with a dorsal fringe of long fine hairs; dark band distally on femora, proximally on tibia. Abdominal terga with 3 longitudinal brown stripes, 1 mesal and 2 lateral; anterior and posterior margins dark; 8 longitudinal rows of dots, 2 mesal and 3 each laterally (Fig. 6). Cerci 70–80% of body length; 28–31 segments, each with posterior whorl of short setae, and one long dorsal and ventral seta; complete dorsal fringe of long hairs after 17th segment.

Egg.—Length 400–450 μm; width 300–350 μm. General shape a prolate spheroid, cross section circular (Fig. 13). Color white. Collar and eclosion line absent (Fig. 13). Chorion covered with irregularly rounded to hexagonal follicle cell impressions (FCI's); FCI walls thick, raised; FCI floors flat with 3–5 medium-sized aeropyles (Fig. 14). Micropylar row subequatorial; orifices with small lips, positioned on FCI floors and walls, some associated with rosettes of 4–5 FCI's (Fig. 14).

Distribution.—This species is known only from the Sierra Nevada foothills, California.

Types.—Holotype male, allotype female, and three paratype nymphs collected from California, El Dorado Co., Indian Creek, 3.3 km NE of Michigan Bar bridge, 13-IV-1987, R. L. Bottorff, deposited in the National Museum of Natural History, Washington, D.C. Paratypes (R. L. Bottorff, collector).—California: Amador Co.: Little Indian Creek, 3 km W of Plymouth, 1 female 18-IV-1986, 1 female 9-V-1986. El Dorado Co.: Indian Creek, 3.3 km NE of Michigan Bar bridge, 97 nymphs 25-III-1987, 21 males, 4 females, 79 nymphs, 6 males & 1 female lab-reared 8-IV-1987, 2 males, 3 females lab-reared 9-IV-1987, 2 males, 4 females lab-reared 11-IV-1987, 17 males, 8 females, 49 nymphs 13-IV-1987, 2 males, 4 females lab-reared 20-IV-1987, 1 male, 2 females lab-reared 23-IV-1987, 1 nymph 10-III-1988; unnamed creek tributary to N bank of Cosumnes River, 2.9 km upstream of Michigan Bar bridge, 4 males, 5 females, 2 nymphs 9-IV-1986, 1 female lab-reared, 1 nymph 10-IV-1986, 2 males

lab-reared 11-IV-1986, 2 females lab-reared 15-IV-1986; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 1 exuvium 1-V-1987. Sacramento Co.: Burgoyne Creek, 1.3 km NE of Michigan Bar bridge, 1 male, 1 female 9-IV-1986, 1 female lab-reared 10-IV-1986, 1 female lab-reared 22-IV-1986, 1 nymph 25-III-1987; Cosumnes River at Michigan Bar, 1 nymph 27-I-1982, 2 nymphs 5-III-1982, 1 nymph 23-IV-1982, 1 male 22-III-1984, 1 male 14-IV-1984, 1 female 22-IV-1984, 1 male, 1 female 11-IV-1986, 1 male 18-IV-1986, 1 male, 1 female 29-IV-1986, 1 male lab-reared 31-III-1986, 1 male lab-reared 5-IV-1986, 1 male & 1 female lab-reared, 1 nymph 11-IV-1986; Cosumnes River at Sloughhouse, 1 nymph 5-III-1982; unnamed creek tributary to S bank of Cosumnes River, 0.3 km upstream of Michigan Bar bridge, 2 males 29-III-1986, 1 male lab-reared, 1 nymph 30-III-1986, 1 female lab-reared 31-III-1986, 1 nymph 25-III-1987. Paratypes are in the collections of the California Academy of Sciences, Brigham Young University, S. W. Szczytko and R. L. Bottorff.

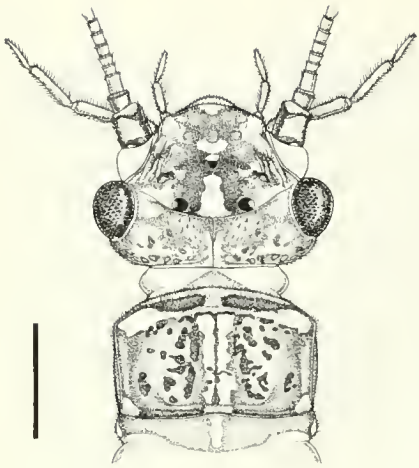
Etymology.—This species is named in honor of the Miwok tribe of California Indians, whose tribal area includes the type locality.

Biological notes.—*Isoperla miwok* primarily occurred in small intermittent streams at lower elevations (20–350 m) of the Sierra Nevada foothills, California. Only a few nymphs were found in nearby larger perennial streams despite extensive searching in these habitats. When this species emerged in March and April, the intermittent streams had low flow and warm water (23–29°C), causing nymphs to exhibit a "push-up" behavior to aid oxygen uptake. Although microhabitats of coarse substrate and fast current were present, mature nymphs usually were collected from pools which had aquatic macrophytes and a silty substrate. Nymphs held in the laboratory several days or weeks at room temperatures (20–25°C) and without water current normally emerged successfully. Emergence started in late March, reached a peak in mid April, and finished by early May, soon after which the stream habitat completely dried. Other Plecoptera found in these intermittent streams included, *Isoperla acula, I. adunca, Oemopteryx vanduzeea* (Claassen), *Suwallia* (new species), *Sweltsa californica* (Jewett), and more rarely, *Cosumnoperla hypocrena* Szczytko and Bottorff. *Isoperla miwok* emerged several weeks before *I. acula* and *I. adunca.*

Diagnosis.—*Isoperla miwok* is placed in the *Isoperla sobria* (Hagen) complex, which has three other western Nearctic species (Szczytko and Stewart 1979): *I. gravitans* (Needham and Claassen), *I. sobria,* and *I. tilasqua* Szczytko and Stewart. It shares the following characteristics with these species: (1) a large body size, (2) male aedeagus membraneous, tubular, and bearing patches of small stout spinulae and longer hair-like spinulae, (3) male vesicle reduced or absent, (4) female subgenital plate truncate or broadly rounded, wide at base, and (5) egg chorion with evenly spaced aeropyles. The male aedeagus of *I. miwok* is most similar to *I. tilasqua* because both have a long apical tube(s). However, *I. miwok* can be separated from all members of this species complex by the pigment patterns of adults and nymphs, the shape and spinule pattern of the male aedeagus, the single long tube on the aedeagus, the shape and pigment of the female subgenital plate, and the collarless egg.

The egg of *I. miwok* is most similar to *I. acula* because both lack a collar and have raised FCI walls, but can be distinguished by its larger overall size, fewer aeropyles in the FCI floors, micropyles with small lips, and some micropyles positioned in FCI floors.

Within this species complex, only *I. miwok* and *I. sobria* occur in California. Both species were found in the same major drainage basin, but were separated by stream type and elevation. *Isoperla miwok* occurred in



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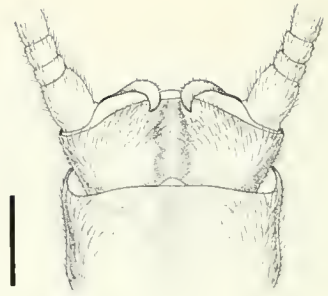

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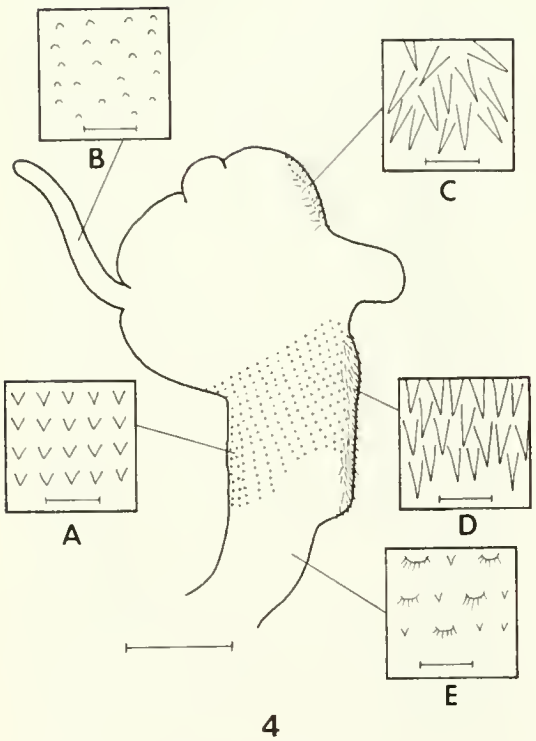

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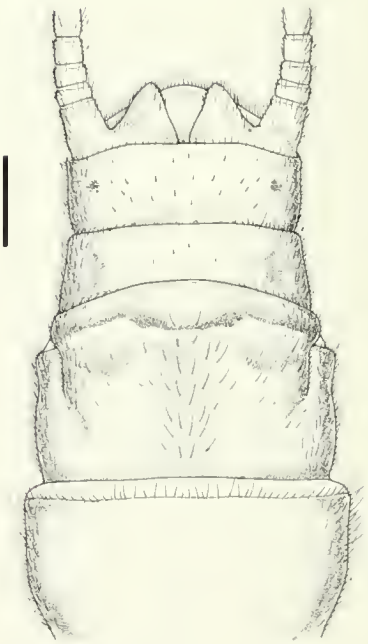

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Figs. 1–5. *Isoperla miwok* adults. 1, Head and pronotum. 2, Male terminalia, dorsal. 3, Male paraproct, lateral. 4, Aedeagus, lateral; A, mesal band of short, stout golden brown spinulae; B, fine rounded spinulae on anteromedian tail-like tube; C, posteroapical patch of large, heavy reddish brown spines; D, posteromesal patch of large, heavy, proximally projecting reddish brown spines; E, proximal patch of fine, shallow scales with microtrichia and fine spinulae. 5, Female subgenital plate, ventral. Scale lines: 1 = 1 mm; 2, 4, and 5 = 0.5 mm; 3 = 0.2 mm; 4A, B, C, D, and E = 25 μm.

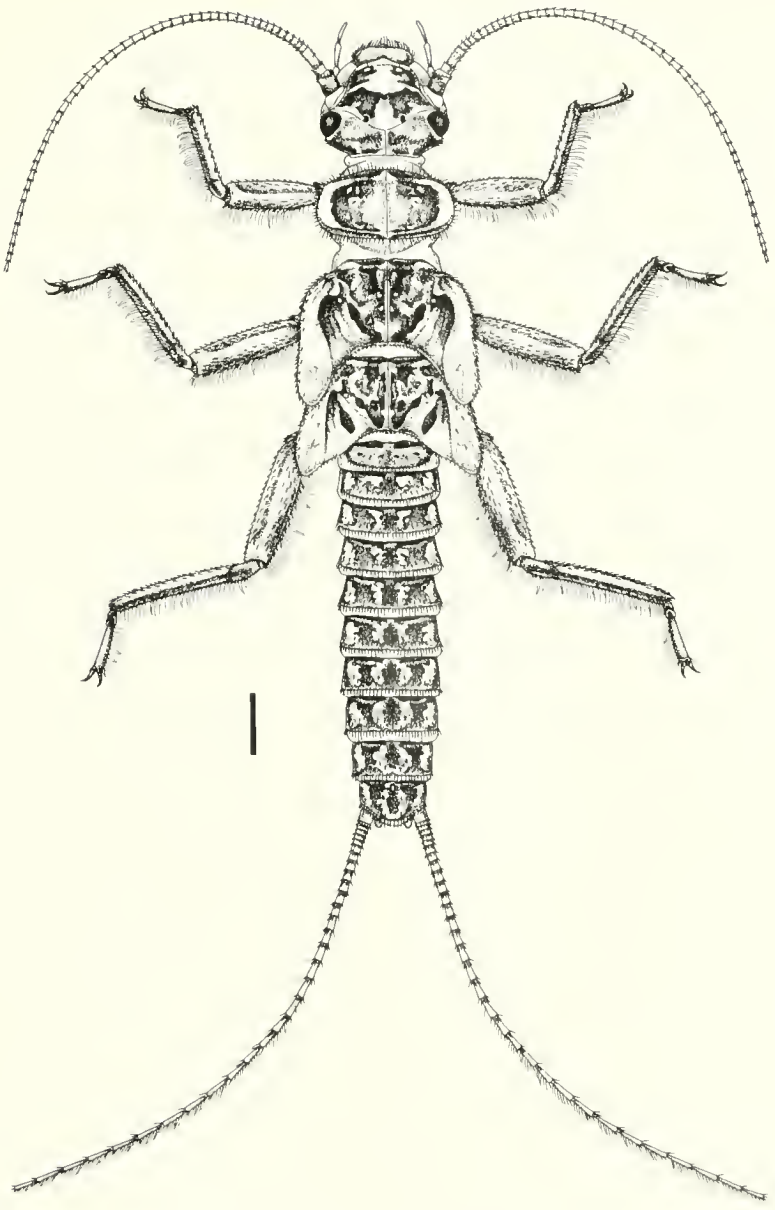


Fig. 6. *Isoperla miwok*, mature nymph, habitus; scale line = 1 mm.

low elevation, intermittent, small streams, while *I. sobria* occurred in medium or high elevation, perennial, small streams. *Isoperla miwok* coexisted with *I. acula* and *I. adunca*, which are in different species complexes, emerged later, and have different drumming calls (Bottorff et al. in press).

Isoperla acula Jewett

Isoperla acula Jewett 1962: 18. Holotype male; Fresno Co., California (CAS).
Isoperla acula Illies 1966: 393.
Isoperla acula Szczytko and Stewart 1979: 77.

Male.—Jewett (1962) and Szczytko and Stewart (1979) have described the male external morphology of *I. acula*. Aedeagus with narrow apical tubular section with sclerotized patch of flat scales which are finely divided anteriorly (Fig. 15B), apex with a small nipple, spinulae absent (Fig. 15); large anteromedian lobe with narrow anterior band of small, fine spinulae (Fig. 15A); mesal section void of spinulae; area below mesal section covered with stout, evenly spaced, proximally projecting, golden brown spinulae (Fig. 15C); proximal area with fine, shallow scales bearing microtrichia (Fig. 15D).

Female.—Macropterous. Body length 10–13 mm; forewing length 11–12.5 mm. Body color and external morphology similar to male. Subgenital plate triangular, produced posteriorly ½ length over 9th sternum; apex variable (normally narrowly rounded, but some broadly rounded, pointed, or rarely notched); mesal patch of long fine setae (Fig. 16).

Nymph.—Body length of mature nymph 10–14 mm. General body color medium brown, covered with dark clothing hairs. Dorsum of head with strongly contrasting pigment pattern (Fig. 17); dark lateral bands extend from ocelli to antennal bases, then anterolaterally; triangular light spot anterior to median ocellus connecting to thin transverse light band across frontoclypeus; interocellar area light; posterior margin of head dark brown, with dark curved bands extending anteriorly to lateral ocelli; stem of epicranial suture light; large irregular light area between each compound eye and lateral ocellus; occiput bearing sinuous row of short spinulae (Fig. 17). Lacinia triangular, bidentate; 1 axillary seta; 20–25 marginal setae below subapical tooth (1 thin seta at tooth base, then 6–8 long equally-spaced stout setae, then 12–16 smaller setae); 3 long stout submarginal setae below base of main tooth, then a narrow continuous band of fine submarginal setae to lacinia base (Figs. 18, 19). Mandibles with 6 teeth, most serrated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 20, 21); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 22, 23). Pronotum with median stripe, disk stripes, and lateral margins light; anterior and posterior margins dark; margins fringed with short and occasional long setae; angles rounded (Fig. 17). Meso-metanota each with 4 dark pointed bars extending posteriorly from anterior margin toward 2 isolated dark bars (Fig. 17). Thoracic sterna with numerous chloride cells (Fig. 26). Legs with a dorsal fringe of long fine hairs; tibia with proximal dark spot. Abdominal terga with 3 longitudinal dark brown bands, median band narrow, lateral bands wide and flared anteriorly and posteriorly (Fig. 17); anterior margin dark; posterior fringe of medium-long setae and scattered intercalary spinulae (Figs. 17, 27, 28). Cercal segments with posterior whorl of short setae; complete dorsal fringe of long hairs after 17th segment.

Egg.—Length 350–370 μm; width 230–260 μm. General shape a prolate spheroid, cross section circular (Fig. 24). Color cream. Collar and eclosion line absent (Fig. 24). Chorion covered with irregularly rounded to pear-shaped FCI's; FCI walls thick, raised; FCI floors flat and finely punctate with 18–28 small aeropyles (Fig. 25). Micropyles subequatorial, associated with rosettes of 4–5 FCI's (Fig. 25).

Distribution.—This species is known only from the Sierra Nevada foothills, California.

Material examined.—California (R. L. Bottorff, collector, except where noted): Amador Co.: Big Indian Creek, 6 km N of Plymouth, 1 male 13-VI to 9-VIII-1982, R. Fouch, 7 nymphs 11-IV-1986, 1 female lab-reared 22-IV-1986, 1 female lab-reared 24-IV-1986, 2 females, 2 nymphs 25-IV-1986,

2 males, 2 females lab-reared 28-IV-1986, 1 male, 3 females 9-V-1986, 1 male lab-reared 12-V-1986, 2 males lab-reared 14-V-1986, 3 females lab-reared 16-V-1986, 1 female lab-reared 17-V-1986, 1 female lab-reared 26-V-1986, 1 female 30-V-1986, 3 nymphs 25-III-1987, 1 female lab-reared, 7 nymphs 1-V-1987; Little Indian Creek, 3 km W of Plymouth, 3 nymphs 18-IV-1986, 11 nymphs 25-IV-1986, 1 male, 2 females 29-IV-1986, 1 female 9-V-1986, 2 males, 1 female 30-V-1986, 24 nymphs 25-III-1987, 18 nymphs 1-V-1987, 6 males, 12 females lab-reared 4-V-1987, 8 males, 9 females, 1 nymph 12-V-1987. Butte Co.: 9 mi. N Oroville, 1 male, 5 nymphs 24-IV-1955, S. W. Hitchcock (USNM). El Dorado Co.: Acorn Creek, 6 km S Pilot Hill, 8 nymphs 3-IV-1988; Cooper Canyon, 3 km W Pilot Hill, 26 nymphs 2-IV-1988; Deadman Creek, 3.8 km SE of El Dorado, 6 nymphs 1-V-1987; Knickerbocker Creek, 5 km NW Pilot Hill, 35 nymphs 6-II-1988; Skunk Canyon, 6 km S Pilot Hill, 1 nymph 3-IV-1988; Sweetwater Creek, 10 km S Pilot Hill, 20 nymphs 3-IV-1988; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 5 nymphs 1-V-1987, 90 nymphs 12-V-1987; unnamed creek tributary to Folsom Lake at Rattlesnake Bar, 6 km SW Pilot Hill, 2 nymphs 2-IV-1988. Fresno Co.: Dry Creek, 7 mi. NE of Academy, 1 male (Holotype, CAS) 19-IV-1955, D. L. Abell. Sacramento Co.: Cosumnes River at Michigan Bar, 1 nymph 5-III-1982, 1 nymph 23-IV-1982, 1 male 31-V-1982.

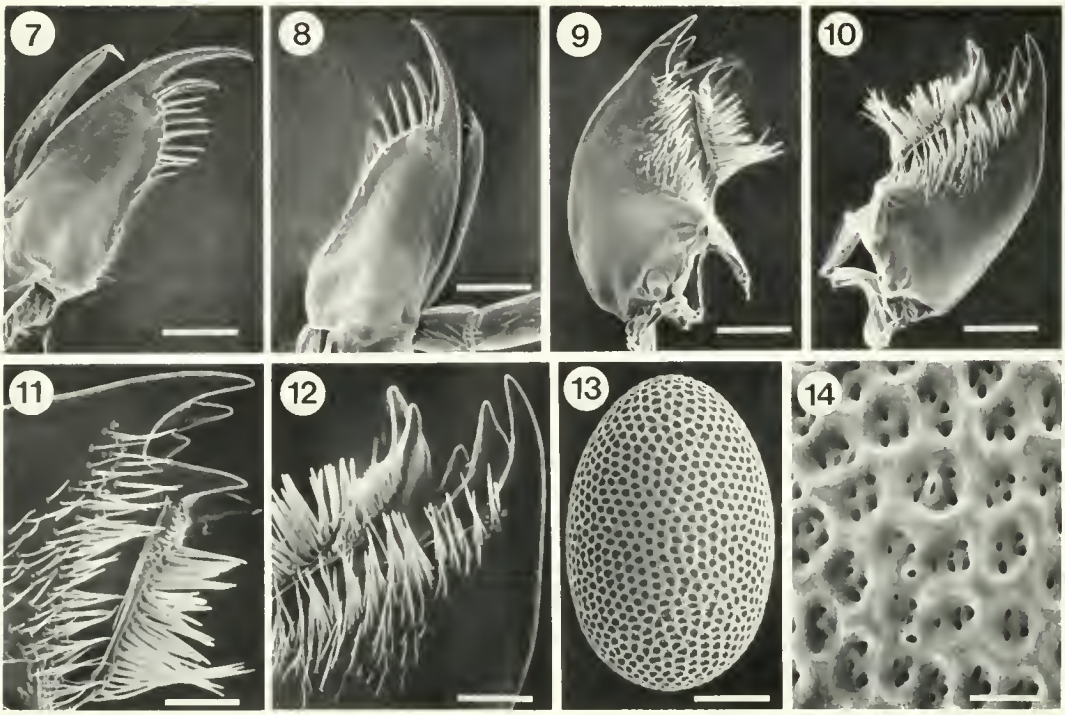
Biological notes.—*Isoperla acula* primarily occurred in small intermittent streams at lower elevations of the Sierra Nevada foothills, California (see Biological Notes for *I. miwok*). Only a few nymphs were found in nearby larger perennial streams. It coexisted with *I. adunca* and *I. miwok*, both members of other *Isoperla* species complexes. Emergence started in mid April, reached a peak in early May, and finished by late May.

Diagnosis.—The phylogenetic relationships of *I. acula* have remained unclear since the original description of the male because of the incomplete aedeagal description, the scarcity of specimens, and the undescribed female, nymph, and egg. Szczytko and Stewart (1979) tentatively placed *I. acula* in the *I. sordida* complex based on the male pigment pattern and Jewett's (1962) partial description of an aedeagal sclerotized structure. It is now clear that *I. acula* males have a band of sclerotized scales which encircle the aedeagus apex, but lack the distinctive sclerotized process which projects from the membraneous aedeagus of all species in the *I. sordida* complex.

Isoperla acula should be included in the *I. quinquepunctata* (Banks) complex, which includes four other western Nearctic species: *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, and *I. quinquepunctata* (Szczytko and Stewart 1979). It shares the following characteristics with these species: (1) 9th and/or 10th male abdominal terga with patches of stout hairs or spinulae, (2) a row of occipital spinulae on nymphal head, (3) a dorsal fringe of long hairs on nymphal legs, and (4) three longitudinal stripes on abdominal terga of nymphs.

Isoperla acula is closely related to *I. mormona* based on similarities in the shape and spination of the male aedeagus, in the bipartite patch of spinulae on the male 9th tergum, and in the pigment patterns of the adult and nymphal head-pronotum. Nymphs will key to *I. mormona* in Szczytko and Stewart (1979). However, *I. acula* can be distinguished from this species by (1) a band of sclerotized scales on the aedeagus, (2) a male vesicle wider than long, (3) male paraprocts long and thin, (4) a triangular female subgenital plate which is produced over sternum 9, (5) larger sized nymphs and adults, and (6) eggs lacking a collar, but with distinct FCI walls.

Isoperla mormona occurs throughout the western Nearctic region, while *I. acula* is restricted to California (Szczytko and Stew-



Figs. 7–14. *Isoperla miwok* nymph and egg. 7, Right maxilla, ventral. 8, Left maxilla, ventral. 9, Right mandible, ventral. 10, Left mandible, ventral. 11, Detail of right mandible, ventral. 12, Detail of left mandible, ventral. 13, Egg. 14, Detail of egg chorion and micropyles. Scale lines: 7, 8, 9, and 10 = 0.2 mm; 11, 12, and 13 = 0.1 mm; 14 = 20 μm.

art 1979). Both species occur at low elevations in the Sierra Nevada, but emerge at different times and inhabit distinctly different stream types. *Isoperla acula* inhabited small intermittent streams, while *I. mormona* inhabited large perennial rivers. The morphological similarity of the two species suggests a recent divergence, possibly associated with the drier climates and increasingly intermittent flow conditions in small streams of the Sierra Nevada foothills following the Pleistocene epoch. Most stoneflies in this region emerge prior to the summer warming of streams; however, *I. mormona* is one of the last to emerge, often when water temperatures exceed 20°C in June–July. The ability of *I. mormona* nymphs to cope with warm water temperatures in perennial streams may have preadapted variants for life in nearby intermittent streams and led to the recent evolution of *I. acula*. The male drumming calls of these two morphologically-similar species are distinctly different in beat number and interval, suggesting that drumming behavior has diverged faster than morphological traits and has been an important isolating factor (Bottorff et al. in press).

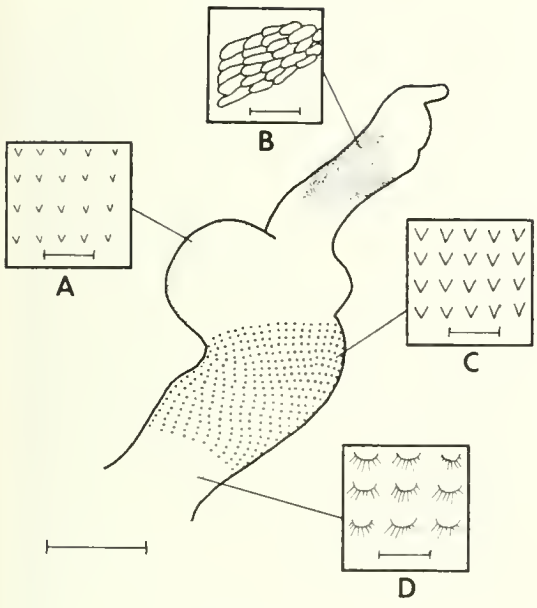
Isoperla adunca Jewett

Isoperla adunca Jewett 1962: 19. Holotype male, allotype female; Santa Clara Co., California (CAS).

Isoperla adunca Illies 1966: 393.

Isoperla adunca Szczytko and Stewart 1979: 80.

Nymph.—Body length of mature nymph 9–12 mm. General body color uniform medium brown. Dorsum of head with a square



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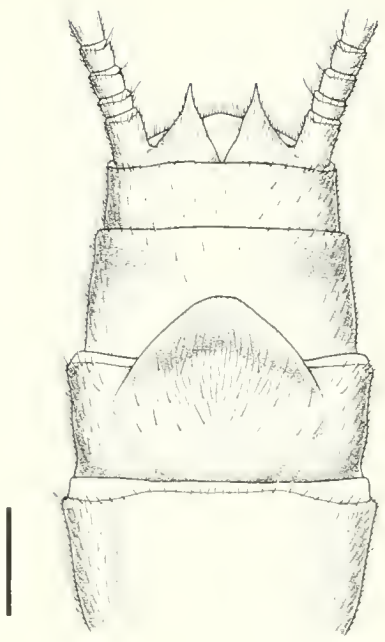

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Figs. 15–16. *Isoperla acula* adults. 15, Aedeagus, lateral; A, anteromedian band of small fine spinulae; B, sclerotized patch of flat scales; C, patch of stout, evenly spaced, proximally projecting golden brown spinulae; D, proximal patch of fine, shallow scales with microtrichia. 16, Female subgenital plate, ventral. Scale lines: 15 and 16 = 0.5 mm; 15A, B, C, and D = 25 μm.

light spot anterior to median ocellus, spot margined laterally by medium brown anteriorly-pointed lobes; light lines extend between lobes and antennal bases; small light spot anterior to lateral ocelli; frontoclypeus with a light transverse band; center of interocellar area light; occiput with reticulations and an irregular row of short spinulae which is interrupted medially (Fig. 29). Lacinia quadrate, bidentate, small gap between bases of main and subapical teeth; 1 axillary seta; definite marginal shelf below subapical tooth with 10–12 stout setae (6–7 long, 4–5 shorter); 8–9 long stout submarginal setae below main tooth, first 3 in gap; scattered marginal and submarginal fine setae extending to lacinia base (Figs. 30, 31). Mandibles with 6 teeth, most serrated; narrow ventral row of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 32, 33); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 34, 35). Antennae light; margin of scape dark. Pronotum uniform brown, lateral margins light; rugosities darker than disks; margins fringed with short and occasional long setae; angles rounded (Fig. 29). Mesometanota brown, with a few light reticulations. Thoracic sterna with mesal sclera lacking dense hairs; membranes with chloride cells (Fig. 37). Legs with a dorsal fringe of long fine hairs. Abdominal terga uniform brown, becoming lighter near pleura, each segment with scattered intercalary spinulae and a posterior fringe of medium length setae (Fig. 36). Cercal segments with a pos-

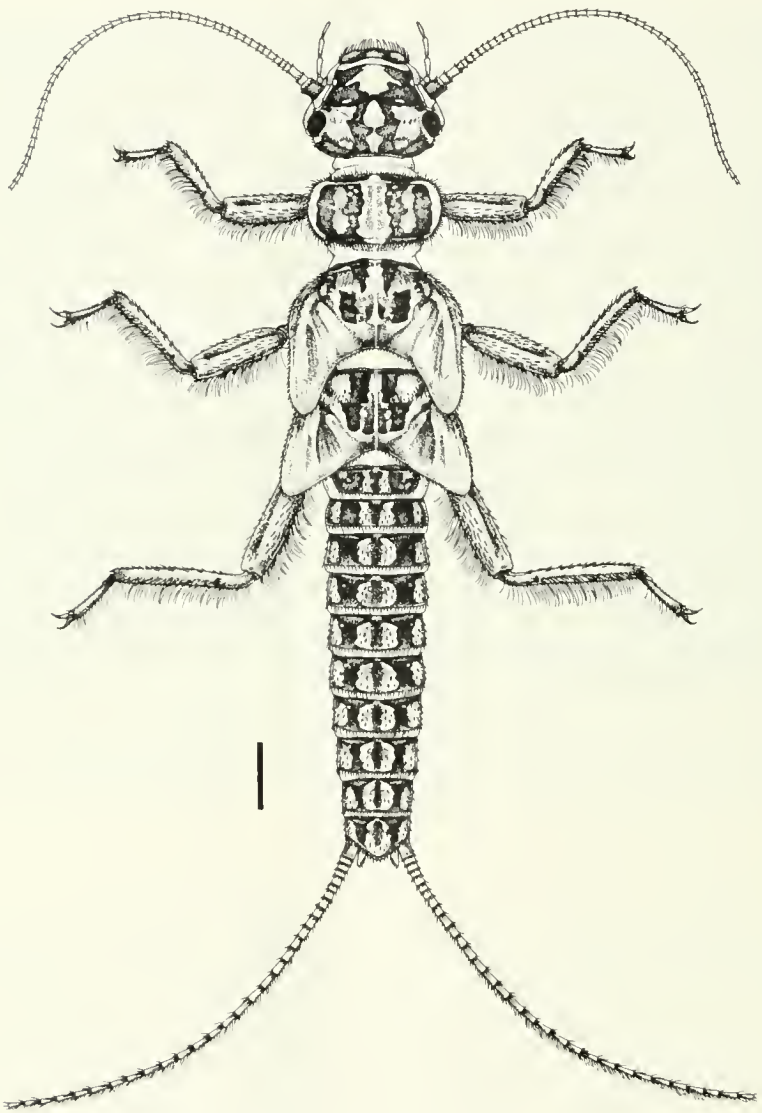
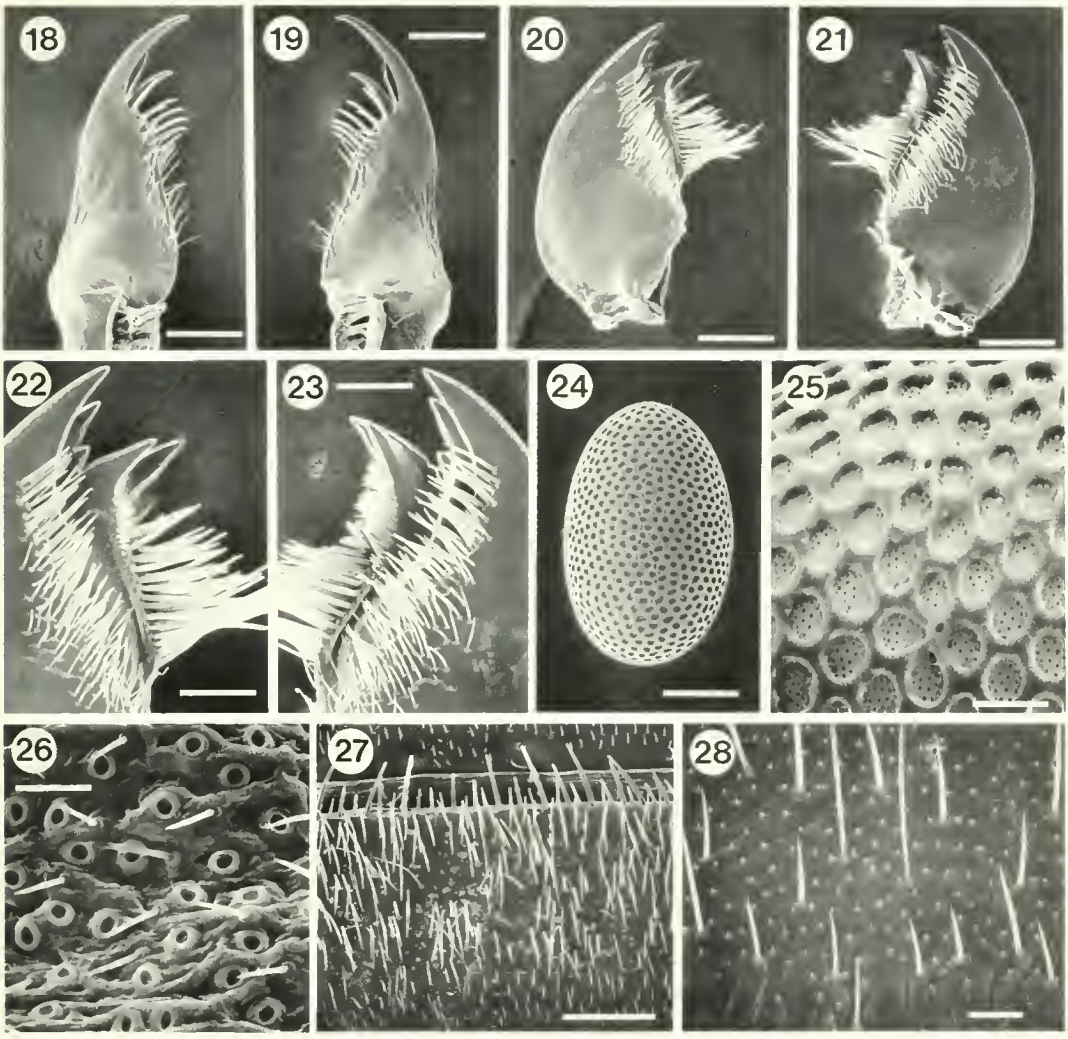


Fig. 17. *Isoperla acula*, mature nymph, habitus; scale line = 1 mm.

terior whorl of short setae and 1 long dorsal and ventral seta; sparse intrasegmental setae, continuous dorsal fringe absent.

Distribution.—This species is known only from the Sierra Nevada foothills and the Coast Range, California.

Material examined.—California (R. L. Bottorff, collector): Amador Co.: Big Indian Creek, 6 km N of Plymouth, 3 nymphs 25-IV-1986, 1 female, 3 nymphs 9-V-1986, 1 female lab-raised 10-V-1986, 1 male, 1 female lab-raised 12-V-1986, 1 female lab-raised 13-V-1986, 4 males, 6 females, 1 nymph 30-V-1986, 2 nymphs 1-V-1987; Little Indian Creek, 3 km W of Plymouth, 10 nymphs 18-IV-1986, 1 male, 5 nymphs 25-IV-1986, 1 male lab-reared, 2 nymphs 27-IV-1986, 1 male, 2 females 9-V-1986, 2 males, 6 females, 5 nymphs 30-V-1986, 2 males, 1 female lab-reared 31-V-1986, 5



Figs. 18–28. *Isoperla acula* nymph and egg. 18, Right lacinia, ventral. 19, Left lacinia, ventral. 20, Right mandible, ventral. 21, Left mandible, ventral. 22, Detail of right mandible, ventral. 23, Detail of left mandible, ventral. 24, Egg. 25, Detail of egg chorion and micropyles. 26, Chloride cells on thoracic sterna. 27, Abdominal terga. 28, Detail of abdominal tergum. Scale lines: 18, 19, 20, 21, and 27 = 0.2 mm; 22, 23, and 24 = 0.1 mm; 25, 26, and 28 = 20 μm.

nymphs 25-III-1987, 3 males, 4 females 1-V-1987, 13 males, 8 females, 62 nymphs 12-V-1987. El Dorado Co.: Acorn Creek, 6 km S Pilot Hill, 1 nymph 3-IV-1988; Cooper Canyon, 3 km W Pilot Hill, 7 nymphs 2-IV-1988; Indian Creek, 3.3 km NE of Michigan Bar bridge, 34 nymphs 25-III-1987, 50 nymphs 8-IV-1987, 1 male, 48 nymphs 13-IV-1987, 1 male, 4 nymphs 21-IV-1987, 6 nymphs 10-III-1988; unnamed N. bank tributary to Cosumnes River, 2.9 km upstream of Michigan Bar bridge, 16 nymphs 9-IV-1986; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 6 nymphs 1-V-1987, 53 nymphs 12-V-1987; unnamed creek tributary to Folsom Lake at Rattlesnake Bar, 6 km SW Pilot Hill, 13 nymphs 2-IV-1988.

Sacramento Co.: Burgoyne Creek, N bank tributary to Cosumnes River, 1.3 km upstream of Michigan Bar bridge, 25 males, 25 females, 27 nymphs 9-IV-1986, 1 male, 1 female lab-raised 10-IV-1986, 1 female 1-V-1986, 6 nymphs 25-III-1987; Cosumnes River at Michigan Bar, 7 nymphs 5-III-1982, 30 nymphs 23-IV-1982, 3 nymphs 21-VI-1982; Cosumnes River at Sloughhouse, 1 nymph 24-IV-1982; unnamed S bank tributary to Cosumnes River 0.3 km upstream of the Michigan Bar bridge, 13 nymphs 21-III-1986, 18 nymphs 29-III-1986, 1 female lab-reared 2-IV-1986, 4 males, 4 females, 10 nymphs, 1 male lab-reared 11-IV-1986, 17 males, 13 females 29-IV-1986, 15 nymphs 25-III-1987; unnamed S bank tributary Cosumnes River 0.7 km downstream of the Michigan Bar bridge, 2 nymphs 14-III-1986, 1 female lab-reared 26-III-1986, 1 male lab-reared 28-III-1986.

Biological notes.—*Isoperla adunca* primarily occurred in small intermittent streams at lower elevations of the Sierra Nevada foothills, California (see Biological Notes for *I. miwok*). Only a few nymphs were found in nearby larger perennial streams. Emergence usually started in late March and extended through April–May, but varied somewhat in different intermittent streams and years as influenced by water temperature and flow duration.

Diagnosis.—Based on the nymphal morphology described in this study, *I. adunca* is retained in the *I. sordida* complex. All nymphs in this group have a pronotal fringe of short stout hairs and occasional longer hairs (Szczytko and Stewart 1979). Additionally, most nymphs in this complex lack a continuous dorsal fringe of long cercal hairs. Based on adult characters, Szczytko and Stewart (1979) found *I. adunca* most closely related to *I. denningi* Jewett; however, the nymph of *I. denningi* is unknown.

Szczytko and Stewart (1979) stated that most Isoperlinae nymphs can be separated from the Perlodinae by the presence of

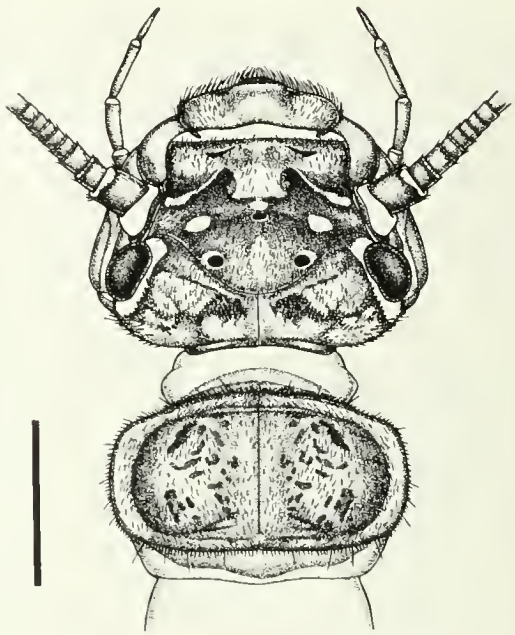
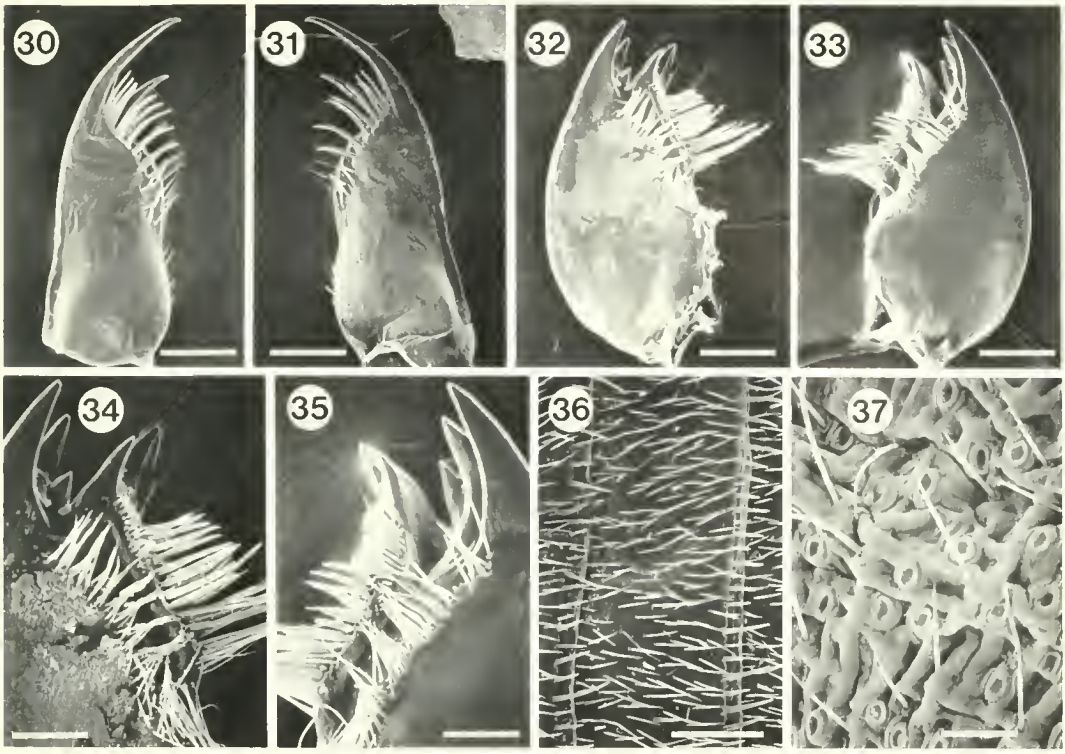


Fig. 29. *Isoperla adunca*, mature nymph, head and pronotum; scale line = 1 mm.

nymphal abdominal stripes. In contrast to all other western Nearctic *Isoperla, I. adunca* nymphs are unique in lacking longitudinal abdominal stripes (some eastern Nearctic species also lack abdominal stripes, including *I. burksi* Frison, *I. marlynia* (Needham and Claassen), and *I. signata* (Banks)). *Isoperla adunca* nymphs also differed from the other *Isoperla* in this study in their mouthpart setation and shape. The lacinia of *I. adunca* has a broad marginal shelf and numerous stout submarginal setae, while their mandibles have a narrow row of ventral setae. These differences were unexpected because Szczytko and Stewart (1979) reported little interspecific variation in the nymphal mouthparts of western Nearctic *Isoperla*.

In the central Sierra Nevada of California, *I. adunca* and *I. bifurcata*, members of the same species complex, occurred in the same major drainage basin, but they emerged at different times and inhabited different stream types. *Isoperla adunca* occurred in



Figs. 30–37. *Isoperla adunca* nymph. 30, Right lacinia, ventral. 31, Left lacinia, ventral. 32, Right mandible, ventral. 33, Left mandible, ventral. 34, Detail of right mandible, ventral. 35, Detail of left mandible, ventral. 36, Abdominal terga. 37, Chloride cells on thoracic sterna. Scale lines: 30, 31, 32, 33, and 36 = 0.2 mm; 34 and 35 = 0.1 mm; 37 = 20 μm.

low elevation, intermittent, small streams, while *I. bifurcata* occurred in medium or high elevation, perennial, headwater springs. *Isoperla adunca* coexisted with *I. acula* and *I. miwok*, which are in different species complexes and have different drumming calls (Bottorff et al. in press).

Isoperla bifurcata Szczytko and Stewart

Isoperla sordida Gaufin et al. 1966: 71.
Isoperla sordida Gaufin et al. 1972: 119.
Isoperla sordida Baumann et al. 1977: 152.
Isoperla bifurcata Szczytko and Stewart 1979: 80. Holotype male, allotype female; Union Co., Oregon (USNM).

Nymph.—Body length of mature nymph 10–13 mm. General body color medium brown, with a median light stripe extending longitudinally along entire dorsum, membranes of fresh specimens reddish and densely covered with chloride cells. Dorsum of head with a dark brown square-shaped band connecting ocelli, dark triangular patches extend posteriorly over occiput; center of interocellar area light; frontoclypeus with a light transverse band; light M-shaped line anterior to median ocellus; large oval light spot posterior to and small light spot anterior to lateral ocelli; occiput with an irregular row of short spinulae (Fig. 38). Lacinia triangular, bidentate; 1 axillary seta; 12–16 marginal setae below subapical tooth (1 fine seta at subapical tooth base, then 5–6 long equally-spaced stout setae, then 6–9 smaller setae); 3 long stout submarginal se-

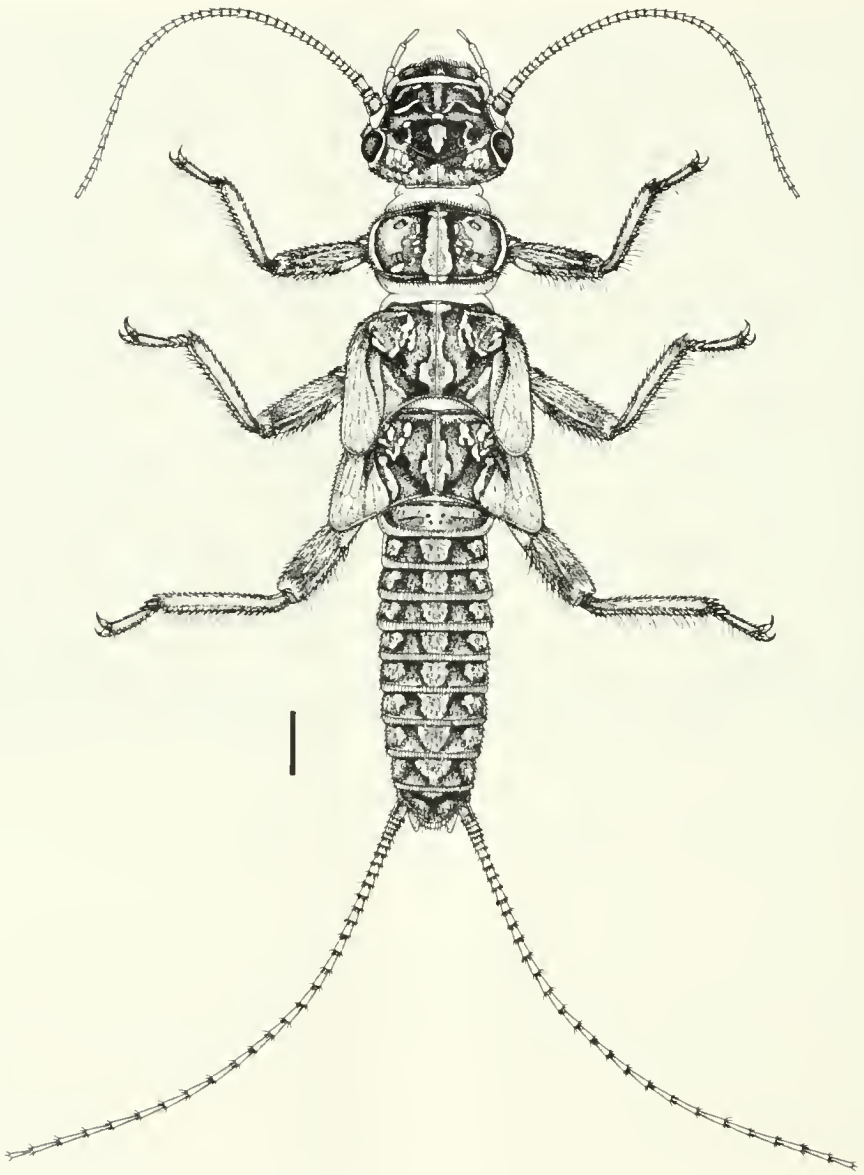


Fig. 38. *Isoperla bifurcata*, mature nymph, habitus; scale line = 1 mm.

tae below base of apical tooth; sparse row of fine marginal and submarginal setae extending to lacinia base (Figs. 40, 41). Mandibles with 6 teeth, most serrated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 42, 43); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 44, 45). Pronotum with light median stripe bordered by dark brown stripes, lateral margins and rugosities light, disks light brown, anterior and posterior margins dark; margins

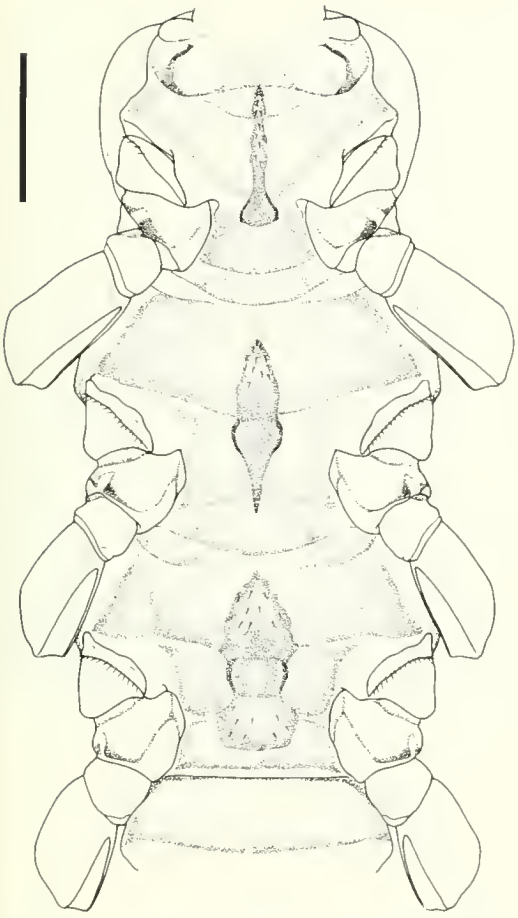


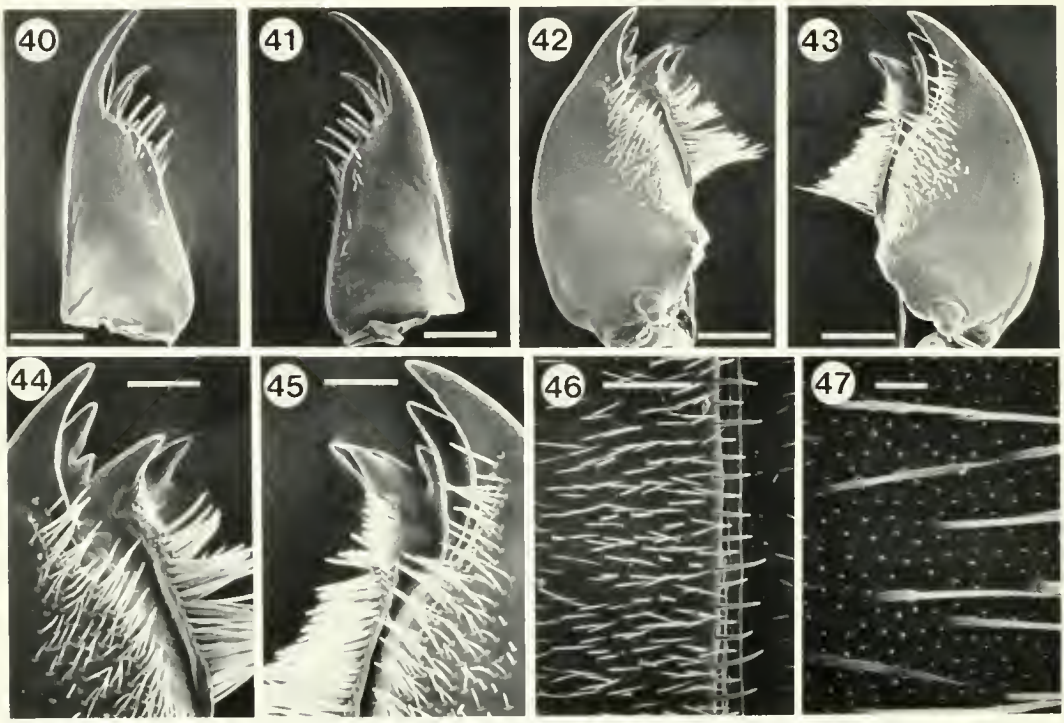
Fig. 39. *Isoperla bifurcata* nymph, thoracic sterna; scale line = 1 mm.

fringed with short stout setae and occasional long setae; angles rounded (Fig. 38). Meso-metanota with light median stripe and reticulations. Meso-metasterna with distinct mesal sclera with dark clothing hairs and patches of stout spinulae (Fig. 39). Legs with sparse dorsal fringe of fine hairs. Abdominal terga with longitudinal median light band and two lateral dark brown bands (Fig. 38); numerous long and short intercalary spinulae (Figs. 46, 47); posterior fringe of medium length setae. Cercal segments with a posterior whorl of short setae and longer ventral seta; sparse intrasegmental setae, continuous dorsal fringe absent.

Distribution.—This species is known from California, Idaho, Oregon, and Washington.

Material examined.—California (R. L. Bottorff, collector): El Dorado Co.: Singleton Springs at headwaters of N Cosumnes River, 25 km E of Grizzly Flat, 3 nymphs 6-VIII-1980, 2 nymphs 15-II-1981, 5 nymphs 27-III-1981, 21 nymphs 24-IV-1981, 10 nymphs 31-V-1981, 25 nymphs 2-X-1981, 15 nymphs 9-III-1982, 37 nymphs 20-IV-1982, 18 nymphs 17-V-1982, 15 nymphs 2-VII-1982; N Cosumnes River, 30–100 m downstream of Singleton Springs, 39 nymphs 6-VIII-1980, 1 female, 15 nymphs 5-IX-1980, 18 nymphs 24-IX-1980, 25 nymphs 31-X-1980, 5 nymphs 26-XII-1980, 6 nymphs 15-II-1981, 20 nymphs 27-III-1981, 6 nymphs 24-IV-1981, 1 nymph 31-V-1981, 109 nymphs 10-VII-1981, 1 male, 1 female, 7 nymphs 16-VIII-1981, 1 female in trap 16-VIII to 2-IX-1981, 74 nymphs 2-X-1981, 9 nymphs 15-XII-1981, 40 nymphs 16-I-1982, 42 nymphs 9-III-1982, 66 nymphs 20-IV-1982, 33 nymphs 17-V-1982, 1 male, 1 female, 59 nymphs 2-VII-1982, 5 males, 4 females 7-VII-1982, 1 male, 3 females 16-VII-1982, 1 male, 1 female 2-VIII-1982, 27 nymphs 10-VIII-1982, 1 female 23-VIII-1982, 12 nymphs 22-VI-1987, 1 male field-reared 9–16-VII-1987, 1 male, 2 females field-reared 16–26-VII-1987, 2 females field-reared 26-VII to 8-VIII-1987; unnamed spring stream tributary to N bank of N Cosumnes River, 2.4 km upstream of Meiss Ranch and 18 km E of Grizzly Flat, 5 nymphs 19-VI-1986, 9 nymphs 30-VI-1986, 15 nymphs 8-VI-1987, 1 male field-reared 8–22-VI-1987, 2 males, 2 females field-reared 22-VI to 9-VII-1987; unnamed N bank tributary to N Cosumnes River, 2.3 km upstream of Meiss Ranch and 18 km E of Grizzly Flat, 1 nymph 14-VI-1986, 1 nymph 18-VI-1986.

Biological notes.—*Isoperla bifurcata* occurred in small spring-fed streams (order 1–2) at medium or high elevations (>1500 m) in the Sierra Nevada, California, and nor-



Figs. 40–47. *Isoperla bifurcata* nymph. 40, Right lacinia, ventral. 41, Left lacinia, ventral. 42, Right mandible, ventral. 43, Left mandible, ventral. 44, Detail of right mandible, ventral. 45, Detail of left mandible, ventral. 46, Abdominal terga. 47, Detail of abdominal tergum. Scale lines: 40, 41, 42, 43, and 46 = 0.2 mm; 44 and 45 = 0.1 mm; 47 = 20 μm.

mally did not coexist with other *Isoperla* species. Emergence started in mid June, reached a peak in July, and continued into August. A few adults were collected in early September, primarily ovipositing females. Other common stoneflies in these habitats included *Soyedina nevadensis* (Claassen) and *Sweltsa borealis* (Banks).

Diagnosis.—Based on the nymphal morphology described in this study, *I. bifurcata* is retained in the *I. sordida* complex because all members have similar pronotal and cercal setation. Szczytko and Stewart (1979) found a close relationship between adults of *I. bifurcata* and *I. fusca* Needham and Claassen. The nymphs of these two species share a similar pattern of longitudinal abdominal stripes and a reduced or absent dorsal fringe of leg hairs. *Isoperla bifurcata* nymphs can be distinguished from all other members in this species complex by their pigment pattern, reduced dorsal fringe of leg hairs, and sclerotized thoracic sterna.

Acknowledgments

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THE STATUS OF THE GENUS *MINEUS* STÅL, 1862 (HETEROPTERA: PENTATOMIDAE: ASOPINAE)

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Abstract.—The synonymy of the genus *Mineus* Stål is confirmed. *Mineus strigipes* is placed in the asopine genus *Perillus* Stål. *Mineus triangularis* (Walker) is transferred to the pentatomine genus *Mormidea* Amyot & Serville, where it is the senior synonym of *Mormidea kirkaldyi* Rolston.

Key Words: *Mineus*, Pentatomidae, Asopinae, taxonomy

The genus *Mineus* was erected by Stål (1867) to hold a single species, *Podisus strigipes* Herrich-Schaefer, 1851. The species occurs throughout the eastern United States with records for New Mexico (Ruckes 1937) and Arizona (Froeschner 1988) probable misidentifications of *Perillus exaptus* (Say). A second species, *Strachia triangularis* Walker, was transferred to *Mineus* by Distant (1900). The locality of origin given by Walker (1867) was Eucador. In his revision of the Asopinae, Schouteden (1907) provided a key to the genera which included *Mineus* and an excellent figure of *Mineus strigipes*. Schouteden listed *Mineus triangularis* with a question mark, and in a footnote he stated that based on Walker's description the species did not appear to belong in *Mineus*. Nothing further has been published on *Mineus triangularis*, and in spite of the excellent drawing, *Mineus strigipes* is often misidentified in collections, being confused with *Perillus exaptus*. The source of the confusion is that Schouteden (1907) and later Torre-Bueno (1938) separate *Perillus* and *Mineus* by the presence of a subapical spine on the profemur. In *Perillus exaptus*, however, the spine is reduced to a small tubercle which in some cases is absent altogether. The dorsal markings are similar enough so that someone using Knight's (1952) revision of *Perillus* would easily confound the two species. It is generally overlooked (e.g. McPherson 1982, Froeschner 1988) that Hoffman (1971) synonymized *Mineus* under *Perillus*, an arrangement with which I am in complete accord. The genitalic structure of *strigipes* is identical to that of the other species of *Perillus*, there being little interspecific variation in either males or females of the genus. McDonald (1966), who studied the genitalia, also concluded that *strigipes* belonged in *Perillus*, but it was not within the scope of his study to make formal nomenclatural changes. The species of *Perillus* can be distinguished by the dorsal markings as described in Knight's (1952) revision and key. *Perillus strigipes* and *Perillus exaptus* can be distinguished because *strigipes* always has a median, longitudinal stripe of yellow to red color on the midline of the pronotum, which is lacking in *exaptus*.

The synonymy of *Mineus* under *Perillus* leaves *Mineus triangularis* without a genus. I recently examined the holotype of *Strach-*

ia triangularis Walker, which is located in the British Museum of Natural History. The species belongs in the genus *Mormidea* Amyot & Serville, subgenus *Melanochila* Stål. The specimen is a female and has an ivory callous traversing the pronotum along the posterior margin of the cicatrices. Also, the specimen has a complete ivory callous along the margins of the scutellum, and a prominent linear ivory callous on the disc of the corium following the embolar suture. The specimen is missing all legs except one which is mounted on a card below it. The tibia is black with a median yellow band. Based on these characters and using the revision of *Mormidea* by Rolston (1978), the species can be placed as *Mormidea montandoni* Kirkaldy, 1902. Subsequently, however, Rolston (1984) reported that *M. montandoni* was misidentified by him and was a senior synonym of *M. bridarolli* Piran, which has the tibia yellow with black spots. The species identified in his revision by having the black tibia with the median yellow band was therefore unnamed and he proposed the name *Mormidea kirkaldyi*. *Strachia triangularis*, with its new combination *Mormidea triangularis* (Walker 1867), is therefore a senior synonym of *Mormidea kirkaldyi* Rolston (1984).

The placement of *Mineus* as a junior synonym of *Perillus* is thus confirmed and the following synonymy is proposed:

1. *Perillus strigipes* (Herrich-Schaefer).
   Podisus strigipes Herrich-Schaefer 1851: 338.
   Mineus strigipes: Stål 1867: 48.
   Perillus strigipes: Hoffman 1971: 55.

2. *Mormidea triangularis* (Walker).
   Strachia triangularis Walker 1867: 323.
   Mineus triangularis: Distant 1900: 55.
   Mormidea kirkaldyi Rolston 1984: 342. **New Synonymy.**
   Mormidea triangularis: **New Combination.**

Acknowledgments

I am grateful to William R. Dolling, British Museum Natural History, for lending the type of *Strachia triangularis* Walker, and David E. Rider for help locating Distant's reference to *Mineus triangularis*.

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TELENOMUS (HYMENOPTERA: SCELIONIDAE) EGG PARASITES OF *ERINNYIS ELLO* (LEPIDOPTERA: SPHINGIDAE)

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Abstract.—*Telenomus dilophonotae* Cameron, *T. connectans* Ashmead, and *T. monilicornis* Ashmead (= *sphingis* auct.) are diagnosed. *Telenomus dilophonotae* (from Costa Rica, Guyana, and Brazil) has been reared from the eggs of *Erinnyis ello* (L.) and *Perigonia stulta* Herrich-Schäffer (Lepidoptera: Sphingidae); *T. connectans* (Florida, Dominican Republic, Grenada, Costa Rica, and Brazil) from *E. ello, Sphinx merops* Boisduval, *Xylophanes tersa* (L.), and *X. neoptolemus* (Stoll) (Sphingidae); *T. monilicornis* has been reared from *E. ello* in Costa Rica and the Dominican Republic. The species *Telenomus puticulus* Johnson is considered a junior synonym of *connectans*.

Key Words: parasitic wasps, *Telenomus, Erinnyis*

The moth *Erinnyis ello* (L.) (Lepidoptera: Sphingidae) is a common Neotropical and southern Nearctic species that often reaches pest status on a number of plants, in particular, manioc (*Manihot esculenta*) and other Euphorbiaceae. The reported egg parasitoids of *E. ello* comprise three species: *Telenomus connectans* Ashmead, *Telenomus dilophonotae* Cameron, and *Telenomus monilicornis* Ashmead. All have previously been recorded as parasites of various sphingids, including *E. ello,* but identification on the basis of the literature has been impossible. They were described around the turn of the century, and no revision or key to the *Telenomus* species of the Neotropical region is available. My objectives are to provide diagnoses of these species to assist in their identification and to present taxonomic notes on the species. The morphological terminology follows that outlined in Johnson (1984) and Bin and Dessart (1983). The biology of *connectans* and *dilophonotae* and the impact upon their host will be discussed in a separate paper by Dr. João Manuel de Abreu.

Telenomus connectans Ashmead

Telenomus connectans Ashmead, 1895: 792, ♂, ♀. Lectotype (examined) in British Museum (Natural History).

Liophanurus connectans: Kieffer, 1926: 79.

Telenomus connectans: Masner, 1965: 111.

Telenomus puticulus Johnson, 1984: 54, ♀. Holotype (examined) in Canadian National Collection of Insects, Arachnids and Nematodes. NEW SYNONYMY.

Diagnosis: Legs, including coxae, and basal antennal segments yellow; occipital carina complete medially; ♀ clava 5-merous, claval formula A11-A7/1,2,2,2,2; ♂ antenna 12-merous; preocellar pit present; T1 with 2–3 pairs of sublateral setae; ♂ genitalia with 3 large teeth per digitus, penis valves and laminae volsellares strongly melanized (Fig. 2; see Johnson 1984 for illustrations of habitus and female antenna).

Telenomus connectans was earlier reported by Gahan (1930) to parasitize the eggs of *E. ello* in the Dominican Republic. Dr. William Haber has also reared this species from the eggs of *Sphinx merops* Boisduval, *Xylophanes tersa* (L.), *X. neoptolemus* (Stoll) and *Perigonia stulta* Herrich-Schäffer in Monteverde, Costa Rica. The species *Telenomus puticulus,* known only from Florida, was described because of the unusual presence of the preocellar pit and multiple pairs of sublateral setae on T1. The first of these structures commonly occurs in the genus *Trissolcus* Ashmead (all of which are parasites of the eggs of Pentatomomorpha), but is extremely rare in *Telenomus* (see Bin and Dessart 1983). In all respects *puticulus* seems to correspond with the abundant Neotropical material now available to me. Thus the distribution of *T. connectans* extends from Brazil through both the Lesser Antilles and Central America to Florida.

The structure of the male genitalia indicates that *connectans* belongs to the *californicus* group of species (large ditigal teeth, laminae volsellares approximated medially, aedeagal lobe short). As I earlier pointed out (Johnson 1984), it is distinguished from practically all of those species by the preocellar pit and sublateral setae. In may respects it is quite similar to species of *Telenomus* that parasitize the eggs of Pentatomidae (Hemiptera), not, however, with the New World species of the *podisi* group, but rather with those of the Old World (e.g. *T. chloropus* Thomson, *T. seychellensis* Kieffer, *T. triptus* Nixon and *T. cyrus* Nixon).

Telenomus dilophonotae Cameron

Telenomus dilophonotae Cameron, 1913: 133, ♀. Holotype (examined) in British Museum (Natural History).

Telenomus dilophonotae: Masner, 1965: 113.

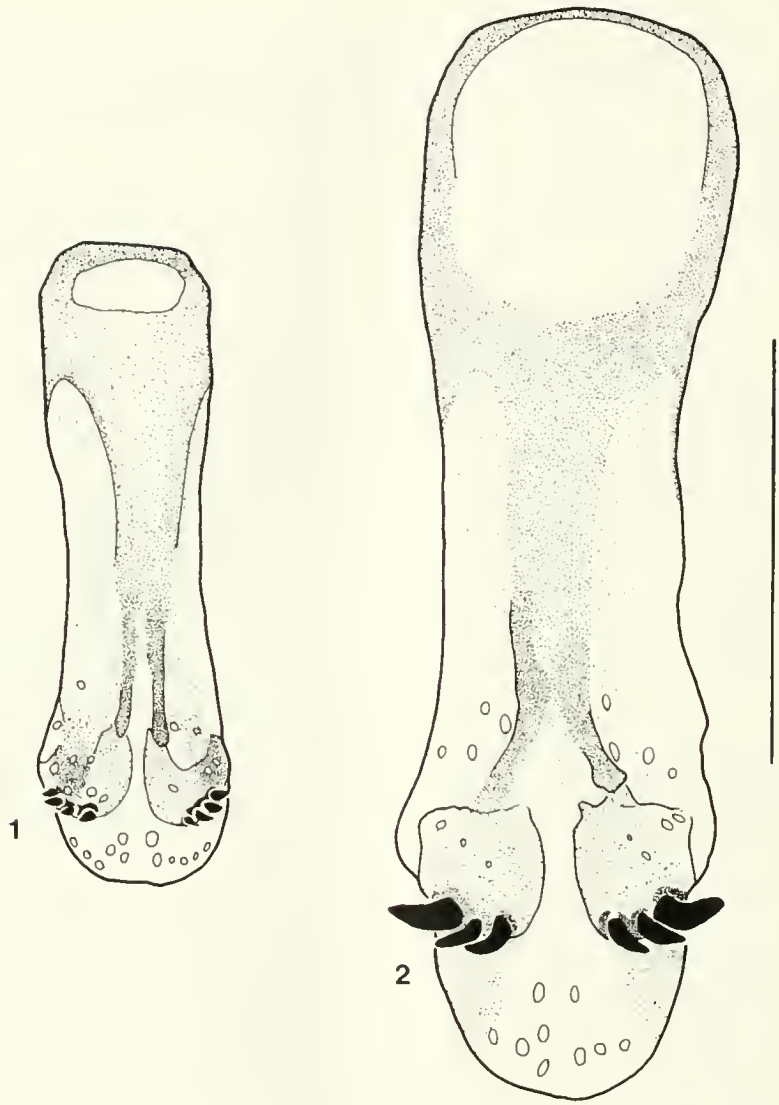
Diagnosis.—Legs and antennae dark brown; occipital carina complete medially; ♀ clava 6-merous (Fig. 3), claval formula (A11-A7/1,2,2,2,2; ♂ antenna 10-merous (Fig. 4); preocellar pit absent; T1 with 1 pair of sublateral setae; ♂ genitalia with 4 small teeth per digitus, generally weakly melanized throughout (Fig. 1).

This species is noteworthy among *Telenomus* in that the female antennal clava is composed of 6 antennomeres (see below), and the male antenna possesses but 10 antennomeres. The genus *Pseudotelenomus* (now considered a synonym of *Telenomus*) was described by Costa Lima (1928) to contain another Brazilian species, *P. pachycoris* (a reduviid egg parasite) in which the male antenna lacked a segment; in this case the fusion of antennomeres is still clearly visible. I can find no indication of fusion in *dilophonotae.* A5 is the sex segment in telenomines generally (see Bin and Vinson 1986) and in *dilophonotae* this segment is unusually enlarged. Thus reduction of antennomeres has occurred distal to this segment. There is some disagreement among workers as to which segments are taken to comprise the clava or club of the female antenna. I am using here the definition outlined in Johnson (1984): I consider A6 to be a clavomere, not because it is greatly broader than the preceding antennomere, but because its apical surface is excavated and parallels the basal surface of A7. The antennae of this species, particularly those of the male, seem to be rather weakly sclerotized and often collapse when air-dried.

Cameron's original description of *dilophonotae* (females only) was based on material reared from *Erinnyis* (then known as *Dilophonota*) in Guyana; Haber has also reared this species from the eggs of *Perigonia stulta* and an unidentified sphingid in Costa Rica (Monteverde, and Santa Rosa National Park in Guanacaste Province).

Telenomus monilicornis Ashmead

Telenomus monilicornis Ashmead, 1894: 203, ♂. Holotype (examined) in British Museum (Natural History).

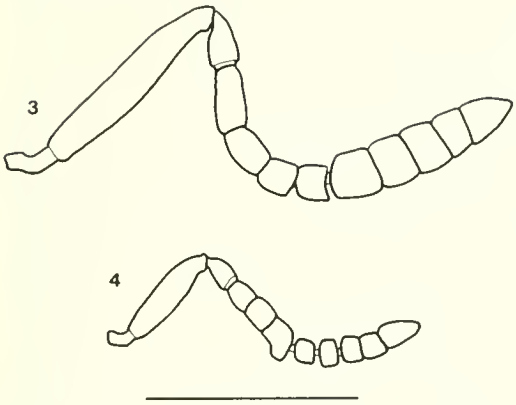


Figs. 1, 2. Male genitalia, ventral view. 1. *Telenomus dilophonotae*. 2. *Telenomus connectans*. Scale line = 0.10 mm.

Telenomus monilicornis: Kieffer, 1912: 22.
Phanurus monilicornis: Kieffer, 1926: 63.
Telenomus monilicornis: Johnson, 1983: 446.
Telenomus monilicornis: Johnson, 1984: 11.

Diagnosis.—Legs and antennae dark brown; occipital carina broadly interrupted medially; ♀ clava 5-merous; ♂ antenna 12-merous; preocellar pit absent; T1 with 1 pair of sublateral setae; ♂ genitalia with four small teeth per digitus, weakly melanized, similar to *T. dilophonotae* (for illustration see Johnson 1984).

Telenomus monilicornis (= *sphingis* auct.) is a widely distributed species, most commonly encountered because it parasitizes the eggs of *Manduca* spp. in the southeastern United States. Ashmead (1887) originally described the species *Teleas sphingis* as a



Figs. 3, 4. *Telenomus dilophonotae*. 3. Female antenna. 4. Male antenna. Scale line = 0.25 mm.

parasite of *Manduca*; however, examination of the holotype proved that this name actually and unfortunately belongs to a species of the *crassiclava* species group, all parasites of the eggs of Homoptera (Johnson 1984). Thus the correct name for this common species is *monilicornis*. I have specimens reared from the eggs of *E. ello* from Costa Rica (Puntarenas, 2 km N Cuatro Cruces) and the Dominican Republic (San Cristóbal).

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A SURVEY OF THE COCCINELLIDAE (COLEOPTERA) ASSOCIATED WITH NURSERY STOCK IN MARYLAND

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Abstract.—Twenty-eight species of adult Coccinellidae were collected in Maryland nurseries from 1986 to 1988. Host plants, presence of prey, and active predation (if any) were recorded for each species. The most commonly detected species were *Coccinella septempunctata* L., *Coleomegilla maculata lengi* Timberlake, and *Hippodamia convergens* Guérin. Coccinellidae populations were seldom high and the number of times beetles were collected was low compared to the number of nurseries visited.

Key Words: host plants, prey

Recently there has been a shift in the pest control practices of commercial nurseries away from cover sprays to spot spraying. Under this new regime, pest control by natural enemies is both desirable and feasible. The Coccinellidae have long been known as major predators of various Homoptera and Acari. Gordon's (1985) treatise on North American Coccinellidae has facilitated adult identification to species. A survey of the Coccinellidae found in Maryland nurseries was undertaken to determine the variety of species present, their frequency of occurrence, and abundances.

Materials and Methods

Adult Coccinellidae were collected during routine nursery inspections. In addition to the typical collection data, host plants, presence and type of prey, and feeding activity by the coccinellids were also noted. Specimens were placed in 70% ethyl alcohol and taken to the laboratory for mounting. Adults were identified by the senior author using Gordon (1985). No efforts were made to identify larvae. Voucher specimens are deposited in the Maryland Department of Agriculture collection.

Results and Discussion

Twenty-eight species representing eighteen genera were collected. Coccinellidae were found in 67 locations in 1986, 82 locations in 1987, and 37 locations in 1988. One reason for the low detection rate in 1988 is that several field personnel only reported unusual coccinellids. Possibly another reason was that the drought conditions and high temperatures during the summer made most adult coccinellids seek protected locations. Prey numbers were also low, possibly due to the same conditions.

Four species were found in high numbers, but most were observed as occasional adults scattered over large areas. The species found are listed below with the counties, host plants (names as listed in Hortus III, 1976), prey associations or feeding activities, and the months in which specimens were collected. The relative frequency of each species is indicated.

Scymninae

Scymnini

Scymnus cervicalis Mulsant: Anne Arundel, Prince George's. *Catalpa* sp., *Quercus* sp. Associated with aphids (Homoptera: Aphididae). May. Two locations.

S. tenebrosus Mulsant: Anne Arundel, Montgomery. *Catalpa* sp., *Malus* sp. Associated with aphids. May. Two locations.

Stethorus punctum punctum (LeConte): Prince George's. *Gleditsia tricanthos* L., *Platanus* sp., *Quercus* sp. April, July. Two locations.

Hyperaspini

Brachicantha felina (Fab.): Montgomery, Prince George's. *Betula* sp., *Malus* sp. Associated with aphids. May, June, August. Four locations.

B. rotunda Gordon: Harford, Montgomery. *Betula* sp., *Malus* sp., *Robinia pseudoacacia* L. Associated with aphids. Four locations.

B. quadripunctata quadripunctata (Melsheimer): Prince George's. May. One specimen.

B. ursina (Fab.): Baltimore. June. One specimen.

Hyperaspis binotata (Say): Baltimore, Prince George's. *Prunus* sp., *Quercus* sp. April, May. Associated with *Melanaspis obscura* (Comstock) (Homoptera: Diaspididae). Two locations.

H. signata signata (Olivier): Anne Arundel, Carroll. May, June. *Juniperus scoruloruum* Sarg. Feeding on *Carulaspis* sp. (Homoptera: Diaspididae). Three specimens.

H. proba (Say): Baltimore, Kent, Prince George's. *Quercus* sp. July, November. Associated with *M. obscura*. Three locations.

Chilocorinae

Chilocorini

Chilocorus kuwanae Silvestri: Specimens of this species were released against various Diaspididae. Recoveries were made in Prince George's and Worcester. *Ilex cornuta* Lindl. & Paxt., *I. crenata* Thunb., *Quercus* spp. Feeding on *Hemiberlesia lataniae* (Signoret), *Lopholeucaspis japonica* (Cockerell), *M. obscura*. Two locations.

C. stigma (Say): Baltimore, Carroll, Howard, Kent, Montgomery, Prince George's, St. Mary's, Somerset. *Acer* sp., *A. palmatum* Thunb., *Euonymus alata* (Thunb.) Sieb., *Fraxinus* sp., *Prunus* sp., *Quercus* sp., *Q. palustris* Muenchh., *Q. robur* L. Associated with *Lepidosaphes yangagicola* Kuwana, *M. obscura, Pseudaulacaspis* sp. (Diasipididae), *Eulecanium cerasorum* (Cockerell) (Coccidae). March, April, May, June, July, September, November. Nineteen locations. This species was common in only one location. All other collections represent only a few individuals.

Exochomus marginipennis (LeConte): Kent, St. Mary's. *Robinia pseudoacacia*. May, November. Two specimens.

Coccidulinae

Coccidulini

Rhyzobius lophanthae (Blasidell): Montgomery. *Pinus* sp. October. One specimen.

Coccinellinae

Coccinellini

Adalia bipunctata (L.): Anne Arundel, Baltimore, Caroline, Carroll, Harford, Kent, Montgomery, Prince George's, St. Mary's. *Acer rubrum* L., *Betula* sp., *Carpinus betulus* L., *Elageanus umbellata* Thunb., *Euonymus alata, Forsythia intermedia* Zab., *G. triacanthos, Lonicera sempervirens* L., *Malus* sp., *Picea abies* (L.) Karst., *Pinus mugo* Turra, *P. strobus* L., *Prunus* sp., *Pyracantha* sp., *Quercus bicolor* Willd., *Rosa rugosa* Thunb., *Salix* sp., *Sorbus acuparia* L., *Spirea nipponica* Maxim., *Viburnum* sp., *V. rhytidophyllum* Hemsl. Feeding on aphids. April, May, June. *Adalia bipunctata* was the fourth most common species found in the survey (47 locations, five commonly).

Anatis labiculata (Say): Anne Arundel, Baltimore, Carroll, Howard, Montgomery,

Prince George's. *Acer rubrum, A. saccharum* Marsh., *Betula* sp., *Cornus florida* L., *Ligustrum* sp., *Pyracantha* sp., *Quercus* sp., *Q. acutissima* Carruth., *Tsuga canadensis* (L.) Carriere, *Ulmus* sp., *Viburnum* sp. April, May, June. Thirteen locations.

A. mali (Say): Harford, Prince George's. *Pinus sylvestris* L. May. Two specimens.

Axion tripustulatum (DeGeer): Prince George's. *Quercus* sp. Associated with *M. obscura.* April. One specimen.

Coccinella novemnotata Herbst: Allegany, Carroll. June, July. Two locations. This species used to be very common in Maryland, judging by the number of specimens in student collections at the University of Maryland and observations by the senior author. Since the introduction of *C. septempunctata* L., the species has only been collected twice in 1986. Whether this is due to a natural decline or competitive displacement is not known at present.

C. septempunctata L.: Allegany, Anne Arundel, Baltimore, Carroll, Charles, Frederick, Harford, Howard, Kent, Montgomery, Prince George's, Queen Anne's, Somerset, St. Mary's, Talbot, Wicomico, Worcester. *Acer saccharum, Betula* sp., *Crategus* sp., *Elageanus umbellata, Euonymus* sp., *Fraxinus* sp., *Hemerocallis* sp., *Ilex cornuta* Lindl. & Paxt., *Juniperus* sp., *Malus* sp., *Pieris japonica* (Thunb.) D. Don, *Pinus* sp., *P. sylvestris* L., *P. thunbergiana* Franco, *Prunus* sp., *Pyracantha* sp., *Pyrus calleryana* Decne., *Rhododendron* sp., *Rosa* sp., *Quercus* sp., *Q. robur, Spirea* sp., *Taxus* sp., *Tilia* sp., *Tsuga canadensis, Viburnum* sp., *Wisteria* sp., *Zelkova serrata* (Thunb.) Makino. March, April, May, June, July, August, September, October, November. This was the most commonly collected species in the survey (87 locations). Feeding on aphids. *Coccinella septempunctata* was taken in large numbers on several occasions. On three separate occasions adult *C. septempunctata* were collected on the bark of cut Christmas trees of *Picea abies, P. pungens* Engelm., and *Pinus sylvestris.* The origin of these trees was eastern Pennsylvania. The movement of cut Christmas trees provides an interesting method of distribution for this species. This species has also been collected in a greenhouse complex.

Coleomegilla maculata lengi Timberlake: Anne Arundel, Baltimore, Caroline, Carroll, Kent, Prince George's, Queen Anne's, St. Mary's, Somerset, Talbot, Wicomico, Worcester. *Acer rubrum, Coreopsis* sp., *Euonymus alata, E. japonica* Thunb., *Forsythia intermedia, Gleditsia tricanthos, Hedera helix* L., *Hibiscus* sp., *Ilex crenata, I. opaca* Ait., *Juglanus* sp., *Magnolia* sp., *Phlox* sp., *Pinus* sp., *P. sylvestris, Prunus* sp., *Pyracantha* sp., *Rosa* sp., *R. rugosa, Quercus* sp., *Salix* sp., *Spirea* sp., *Taxus* sp., *Tsuga canadensis, Vitis* sp., *Z. serrata.* Feeding on aphids; associated with *Pineus strobi* (Hartig) (Homoptera: Phylloxeridae) and *Dymicoccus wisteriae* (Green) (Pseudococcidae). April, May, June, July, August. This was the second most common species in this survey (45 locations).

Cycloneda munda (Say): Anne Arundel, Baltimore, Charles, Harford, Montgomery, Prince George's, Queen Anne's, Wicomico. *Acer* sp., *Betula pendula* Roth, *Malus* sp., *Pyracantha* sp., *Quercus palustris* Muenchh., *Taxus* sp. Feeding on aphids. May, June, July, August. Fifteen locations.

Olla v-nigrium (Mulsant): Anne Arundel, Prince George's, Talbot, Worcester. *Magnolia* sp., *Ulmus* sp. Associated with *Toumeyella liriodendri* (Gmelin) (Homoptera: Coccidae). May, June, September. Five locations.

Hippodamia convergens Guérin: Anne Arundel, Baltimore, Carroll, Frederick, Harford, Kent, Montgomery, Prince George's, St. Mary's, Washington, Wicomico, Worcester. *Acer rubrum, Cornus florida, Elageanus umbellata, Euonymus alata, Fraxinus* sp., *Hedera helix, Hibiscus syriacus* L., *Hydrangea* sp., *Juglanus* sp., *Malus* sp., *Picea abies, Prunus* sp., *Pyracantha* sp., *Quercus* sp., *Rosa* sp., *Viburnum* sp. Feeding on aphids. April, May, June, August.

This was the third most common species collected (39 locations).

H. glacialis (Fab.): Kent, Somerset. July. Two locations.

Mulsantia picta (Randall): Caroline, Howard, Kent. May, June. Three specimens.

Neoharmonia venusta venusta (Melsheimer): Anne Arundel. *Salix* sp. May. One specimen.

Psylloborini

Psyllobora vigintimaculata (Say): Charles, Kent. May, September. Three locations.

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ANOMALIES IN CORNICLES OF APHIDS (HOMOPTERA: APHIDIDAE)

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Abstract.—Anomalies in number, size, shape, and other characteristics of cornicles (siphunculi) of aphids are described and illustrated. Variations range from complete absence of cornicles to a total of four in species that normally have two cornicles.

Key Words: Aphididae, cornicles, anomalies, aphids

This article portrays assorted anomalies in cornicles (siphunculi) of aphids. The recorded aberrations occur in 14 species that typically have two similar, tubelike cornicles and in one species that has truncate cornicles. Abnormalities in cornicles occur infrequently but they are not rare, and they are seldom mentioned in literature, a condition that appears to justify a short treatment of the subject.

Modifications in cornicles may be in numbers, size, shape, imbrications, reticulations, apical openings, and flanges. Variations in number are less frequent than other abnormalities. Flanges are absent when apices of cornicles are almost or completely closed. The closing of cornicle apices doubtless is detrimental to survival of the insects, as was indicated by Dixon and Stewart (1975) who stated that exudates from the cornicles drove away predators. Earlier, Nault, Edwards and Styer (1973) indicated that cornicles of certain species emit pheromones that repel other insects from feeding sites.

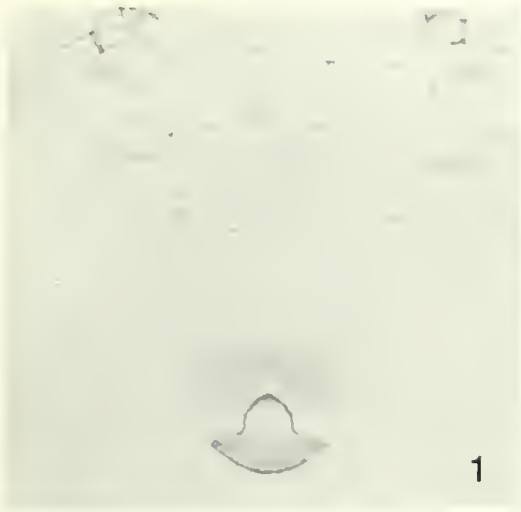
Abnormalities are sometimes present in more than one individual of a collection and other abnormalities may occur in specimens with modified cornicles. We noted aborted antennae in two species with abnormal cornicles.

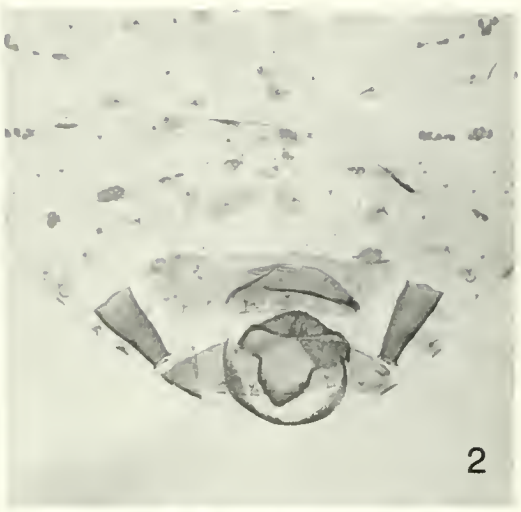
Species without Cornicles

One intermediate vivipara of *Dysaphis foeniculus* (Theobald) (Fig. 1) (on *Daucus carota* L., Heyden Trust, Sandy's Parish, Bermuda, 24-III-1988, D. J. Hillburn, M. J. Mello, M. B. Stoetzel) is devoid of cornicles, while other specimens (Fig. 2) of the lot have two normal ones.

Species with One Cornicle

An alate vivipara of *Hyalopterus pruni* (Geoffroy) (Fig. 3) (on an unidentified plant, Bombay Hook, Delaware, 25-VI-1975, G. Angelet) has one typical cornicle. An apterous vivipara of *Aphis masoni* Richards (Fig. 4) (sweeping mixed meadow, Churchill, Manitoba, Canada, 24-VII-1975, A. G. Robinson) also has one normal cornicle. In an alate vivipara of *Myzus ascalonicus* Doncaster (Fig. 5) (on *Sedum* sp., England, intercepted at Seattle, Washington, 8-V-1972, J. D. Kail), the one cornicle is ⅛ shorter and more slender than the cornicles in another alata from the same collection; it is slender throughout, irregular in shape, and rounded apically with a minute opening. Stoetzel (1986) apparently was the first to record the presence of only one cornicle in an aphid, *Cinara terminalis* (Gillette and Palmer).





Figs. 1–2. *Dysaphis foeniculus.* 1, Intermediate vivipara without cornicles. 2, Apterous vivipara from same collections with normal cornicles.

Fig. 3. *Hyalopterus pruni.* Alate vivipara with only one cornicle.

Fig. 4. *Aphis masoni.* Apterous vivipara with only one cornicle.

Fig. 5. *Myzus ascalonicus.* Alate vivipara with only one cornicle.

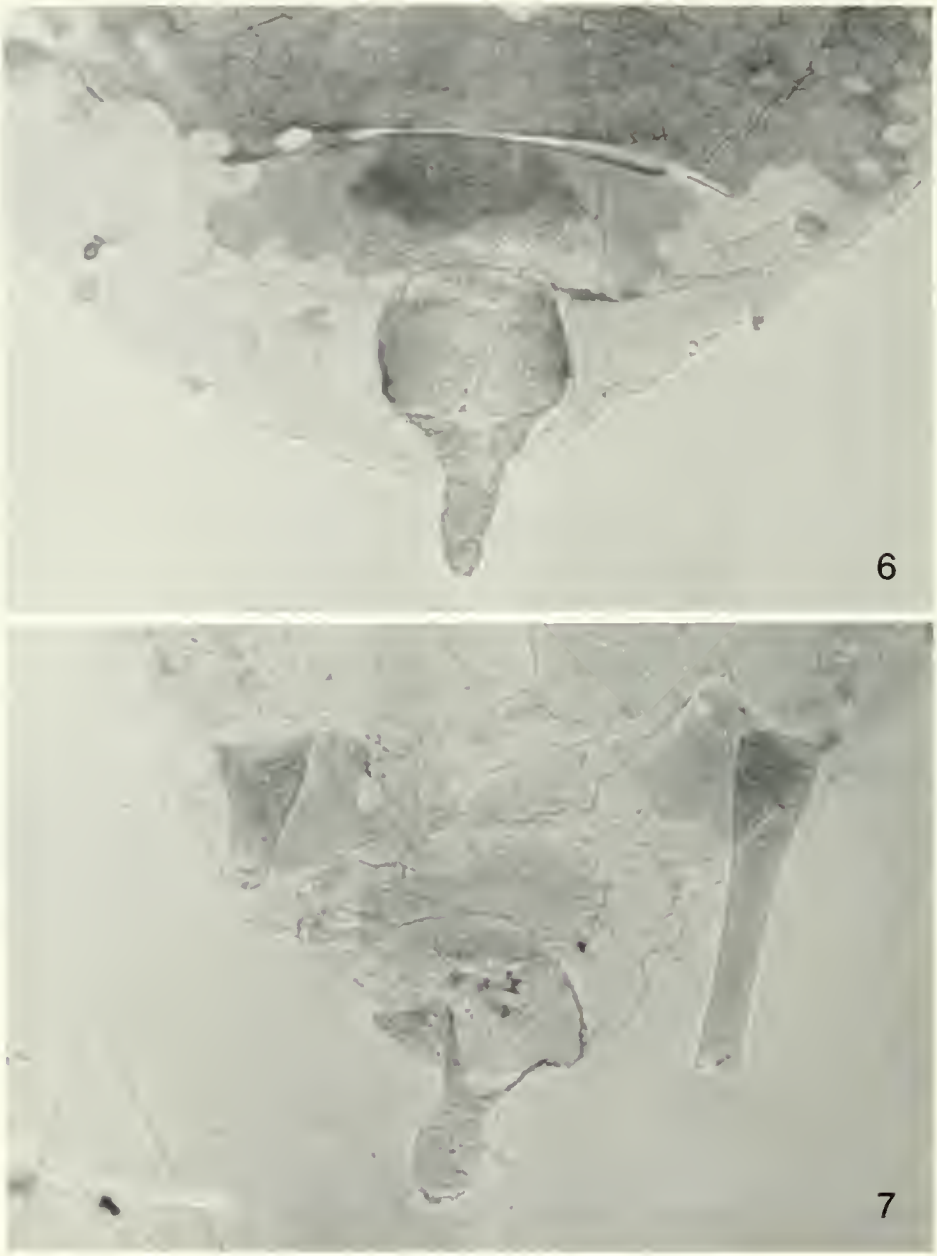
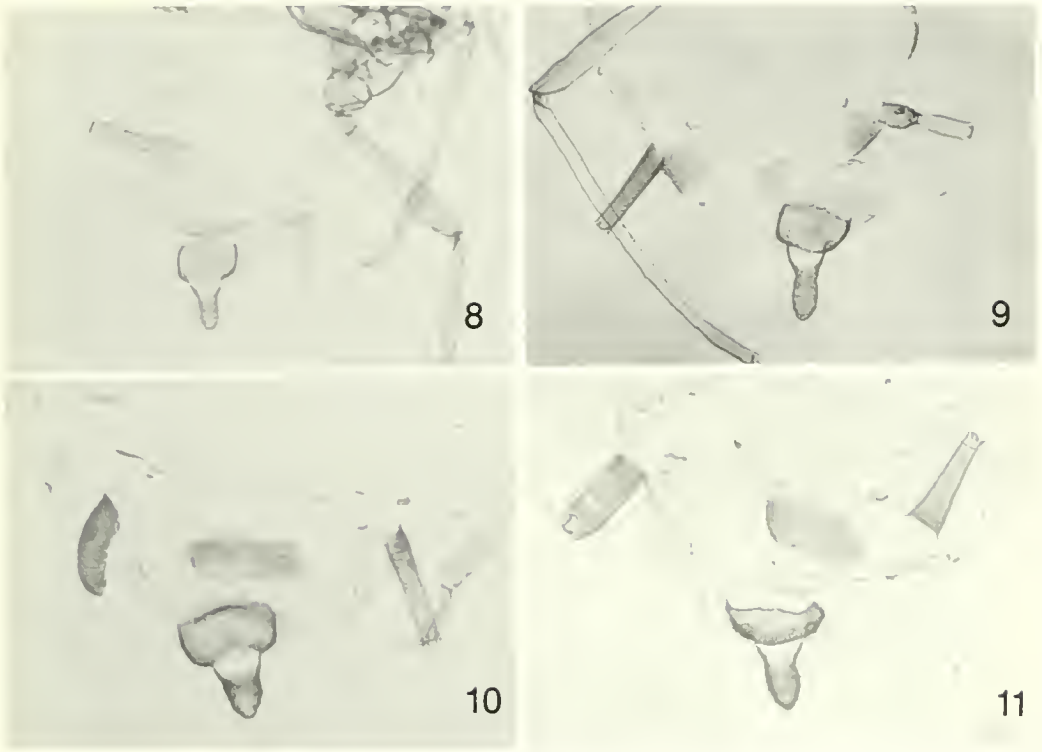


Fig. 6. *Aphis craccivora*. Apterous vivipara with dwarfed, nipple-shaped cornicles.
Fig. 7. *Aphis spiraecola*. Alate vivipara with one cornicle shortened and rounded apically.

Species with Two Cornicles

When two cornicles are present, one or both may be modified. In an apterous vivipara of *Aphis craccivora* Koch (Fig. 6) (on *Verbascum thapsus* L., Athens, Georgia, 4-V-1973, O. R. Pagus), both cornicles are most unusual in that they are no longer than their basal diameters and are nipple-shaped, with apices closed. In an alate vivipara of

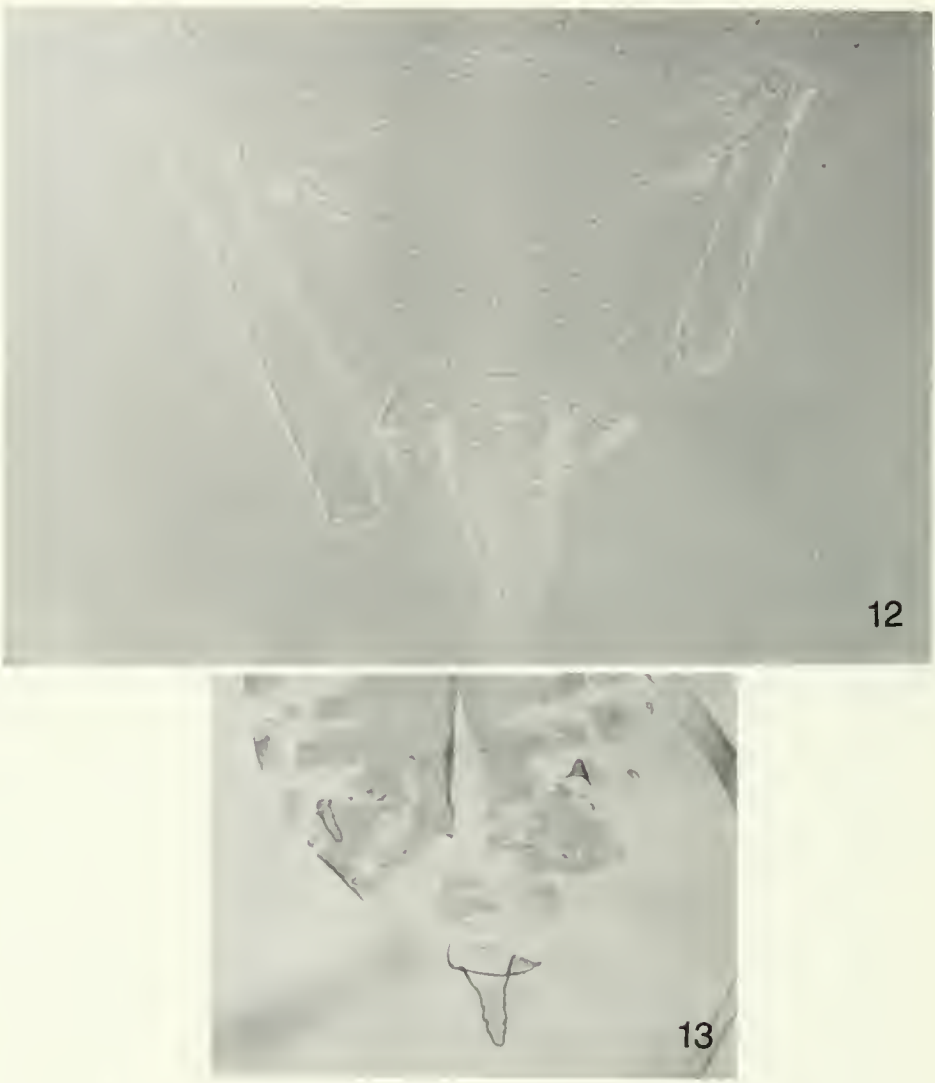


Figs. 8–9. *Aphis spiraecola*. 8, Alate vivipara with one cornicle narrowed at midlength. 9, Alate vivipara with one cornicle strongly constricted just proximad of midlength.

Figs. 10–11. *Aphis fabae*. 10, Apterous vivipara with one cornicle curved and unusually stout. 11, Apterous vivipara with one cornicle abnormally wide and with a conspicuous hole in its lower surface.

Aphis spiraecola Patch (Fig. 7) (on *Prunus lyonii* (Eastw.) Sarg., Arcadia, California, 22-III-1966, H. G. Walker), one cornicle is about ½ the length of the normal one, is rounded, and apparently is closed apically. An alate vivipara of *Aphis spiraecola* Patch (Fig. 8) (on *Taxodium distichum* (L.) L. Rich., Chevy Chase, Maryland, 1-VI-1976, E. J. Hambleton) has one cornicle that tapers to its midpoint and then enlarges to its end; it is slightly shorter than the normal one, has few imbrications, and its apex has an opening but lacks a flange. Another alate vivipara of *A. spiraecola* (Fig. 9) (on *Malus* sp., Princess Anne, Maryland, 20-VI-1968, C. W. McComb) has one cornicle of nearly normal length that is strongly constricted just proximad of its midlength, has very few imbrications, and has a typical apical opening but lacks a flange. A second alate vivipara (not shown) of this collection has one cornicle that is ½ the length of the normal one, has few imbrications, and is rounded and closed apically. An apterous vivipara of *Aphis fabae* Scopoli (Fig. 10) (on *Papaver orientale* L., Polur, Iran, 16-VII-1974, G. Buckingham) has a curved cornicle that is somewhat shorter and stouter than the normal one and apparently is closed apically. In another apterous vivipara of *A. fabae* (Fig. 11) (on *Papaver* sp., Greeley, Colorado, IX-1932, W. J. Zaumeyer), one cornicle is slightly shorter than the other and has a subcircular hole in its lower surface; it has a slight indication of a flange.

An apterous vivipara of *Myzus persicae* (Sulzer) (Fig. 12) (on *Blechnum occidentale* L., Arcadia, California, 26-III-1969, H. G.



Figs. 12–13. *Myzus persicae*. 12, Apterous vivipara with one cornicle shortened and club-shaped. 13, Alate vivipara with one cornicle finger-shaped and one somewhat thimble-shaped.

Walker) has a shortened, club-shaped cornicle that is closed apically. In an alate vivipara of *M. persicae* (Fig. 13) (from yellow pan trap, Fort Kent, Maine, 25-VII-1974, F. R. Holbrook), both cornicles are much less than normal length; one is somewhat thimble-shaped and the other finger-shaped; they have few imbrications and their apices are closed. Antennae of this insect terminate abruptly at the end of the fifth segments; the primary sensorium is present in one antenna and absent from the other. In an alate vivipara of *Nasonovia ribisnigri* (Mosley) (Fig. 14) (on *Lactuca sativa* L., Spain, intercepted at New York, New York, 1-V-1967, F. Planer), one cornicle is ½ the length of the normal one and tapers gradually to an acute, closed tip; its distal portion is devoid of imbrications. In an apterous vivipara of *Dactynotus sonchi* (Geoffroy) (Fig. 15)

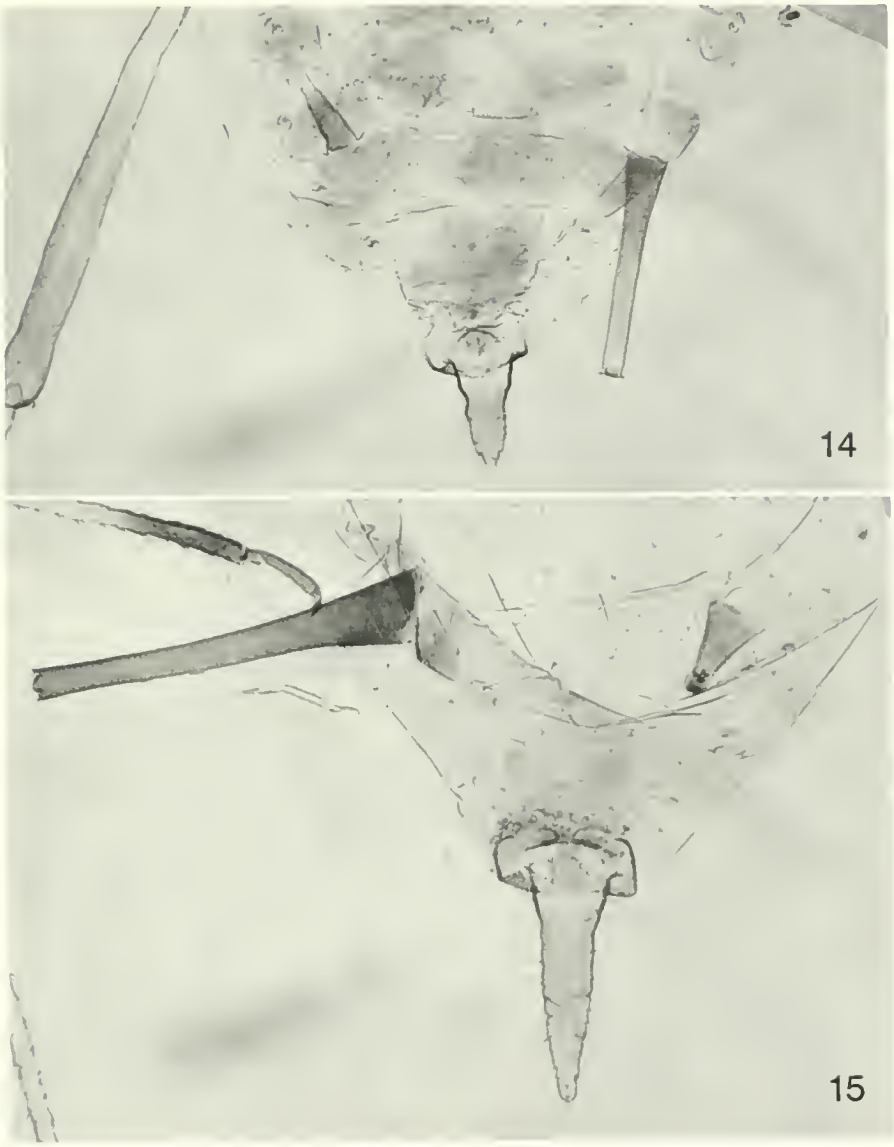
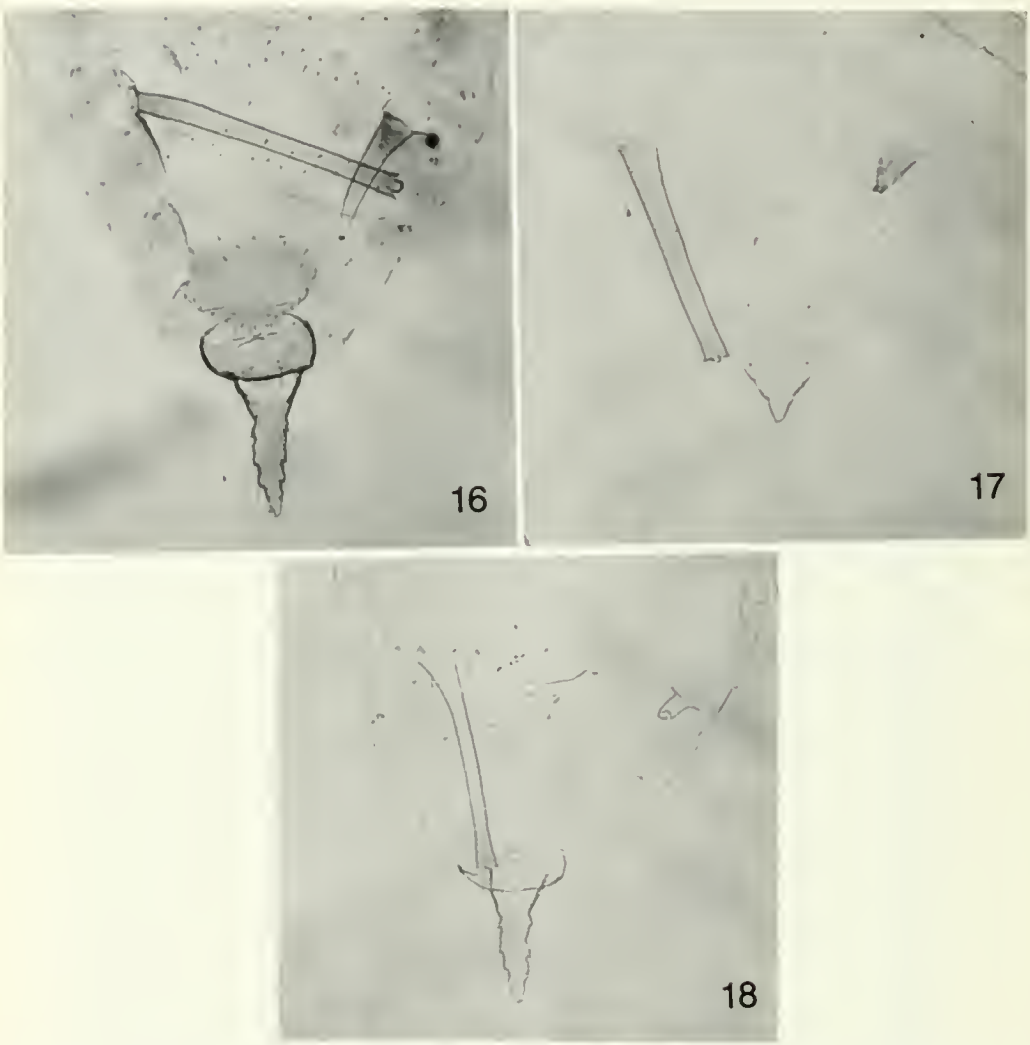


Fig. 14. *Nasonovia ribisnigri.* Alate vivipara with one cornicle shortened and tapered.
Fig. 15. *Dactynotus sonchi.* Apterous vivipara with one cornicle shortened and knobbed apically.

(on *Sonchus oleraceus* L., Honolulu, Hawaii, 20-VI-1975, R. Mau), one cornicle is ¼ the length of the normal one, tapers, then enlarges and terminates in a knob; the presence or absence of a terminal opening cannot be determined because of debris. The cornicle has imbrications but lacks reticulations.

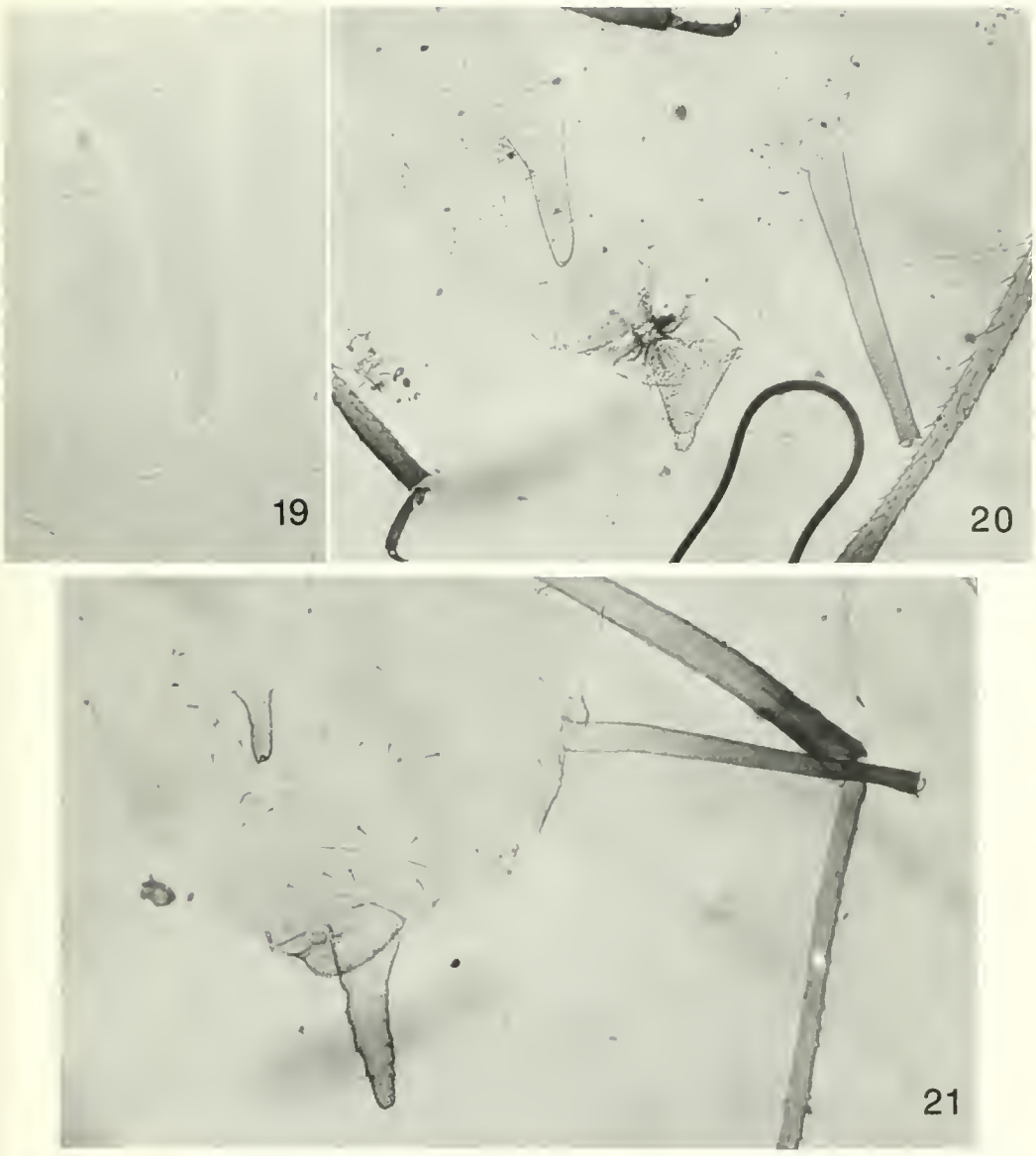
In two specimens of *Acyrthosiphon kondoi* Shinji (on *Medicago sativa* L., Quetta Valley, Pakistan, 19-VI-1978, S. Hamid), one cornicle in an alate vivipara (Fig. 16) is about ½ the length of the normal one and is constricted near its fingerlike end which has a small opening but no flange. In an alatoid nymph (Fig. 17), one greatly abbre-



Figs. 16–18. *Acyrthosiphon kondoi*. 16, Alate vivipara with one cornicle shortened and tapered. 17, Alatoid nymph from same collection with one cornicle dwarfed and bearing a stublike protrusion on its distal margin. 18, Alate vivipara with one cornicle greatly dwarfed.

viated cornicle lacks imbrications and a flange; it has a stublike extrusion on its distal margin. And in another alate vivipara of *A. kondoi* (Fig. 18) (on *Medicago sativa* L., St. George, Utah, 11-V-1975, D. Huber), one cornicle is a stub no longer than the basal diameter of the normal cornicle; it has few imbrications and an apical opening but it lacks a flange.

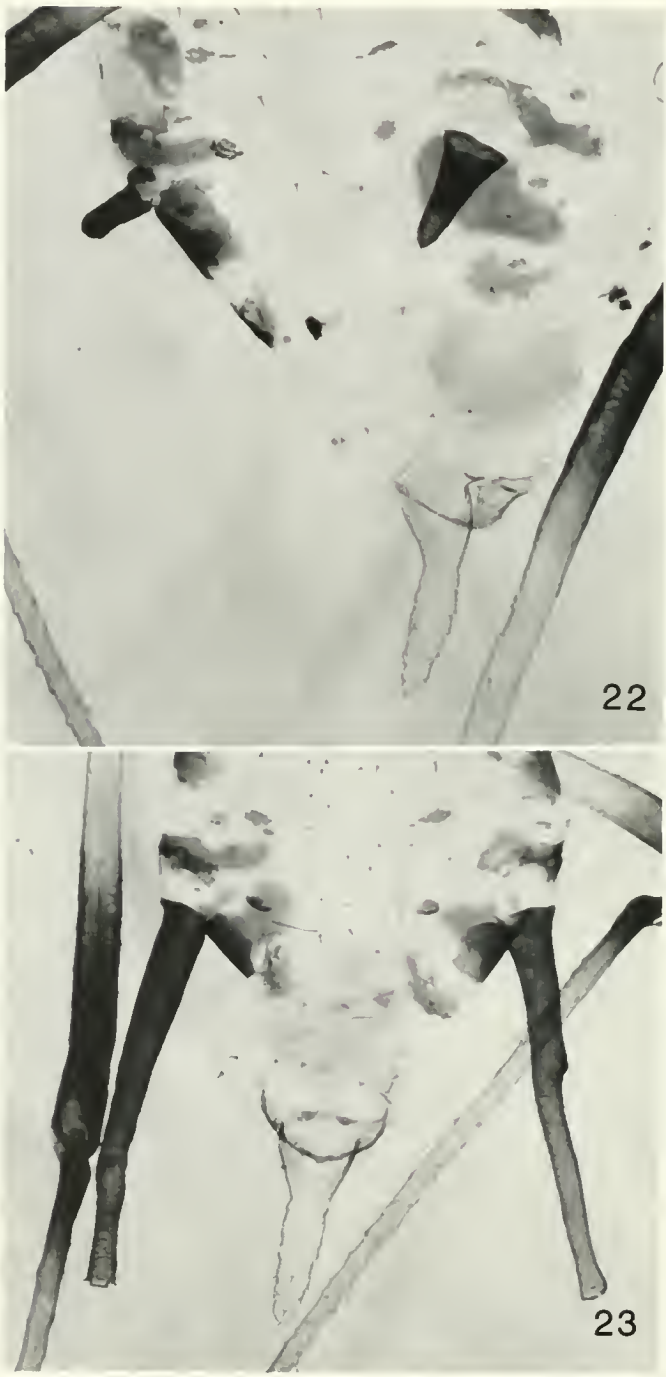
In an apterous intermediate of *Macrosiphum euphorbiae* (Thomas) (Fig. 20) (on *Rosa* sp., England, intercepted at Philadelphia, Pennsylvania, 10-VI-1964, F. Harvey and N. Arehart), one cornicle is about ½ the length of the normal one, tapers slightly to a rounded, closed apex, and has few imbrications but no reticulations. There is a transverse, oblong opening on its dorsal surface (Fig. 19). This specimen has an atypical cauda, the apex of the abdomen resembling that of a nymph instead of an adult. In an alate vivipara of *M. euphorbiae* (Fig. 21)



Figs. 19–21. *Macrosiphum euphorbiae*. 19, Abnormal cornicle of apterous intermediate enlarged to show hole in its upper surface. 20, Apterous intermediate with one cornicle modified. 21, Alate vivipara with one cornicle dwarfed.

(from yellow pan trap, Beltsville, Maryland, 10-X-1975, W. W. Cantelo), a cornicle dwarfed to about ¼ normal length has few imbrications, no reticulations and a small apical opening without a flange.

Two alate viviparae of *Macrosiphum rosae* (L.) (on greenhouse roses, New Brunswick, New Jersey, 28-X-1975, H. T. Streu) have modified cornicles and antennae. In one specimen (Fig. 22), the cornicles are greatly shortened and their ends are closed; one tapers gradually and is pointed apically while the other is of nearly uniform diameter and is rounded apically; both have few



Figs. 22–23. *Macrosiphum rosae*. 22, Alate vivipara with both cornicles dwarfed and mis-shaped. 23, Alate vivipara from same collection with both cornicles atypical in shape.

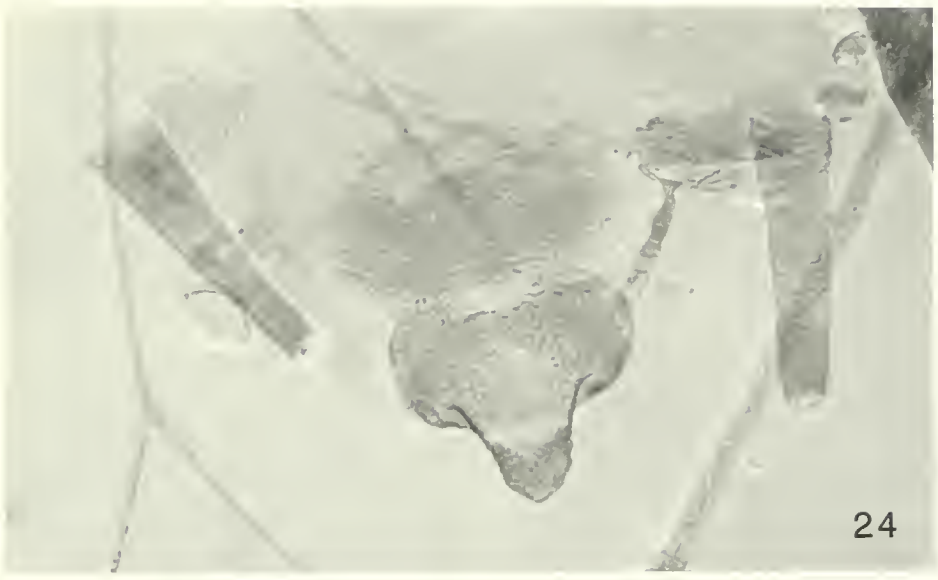


Fig. 24. *Aphis sambucifoliae.* Alate vivipara with three cornicles, one greatly reduced in size proximad of a normal one.

Fig. 25. *Euceraphis punctipennis.* Alate vivipara with four cornicles, the anterior pair normal, the posterior pair supplementary.

imbrications and no reticulations. In this insect, one antenna terminates and is weakly nipplelike at the end of the fourth segment; the other antenna is slightly shorter and is curved with an invagination at its end. In the other specimen (Fig. 23), one of the unusually slender cornicles is narrowed abruptly, has four indistinct rows of reticulations, an abnormal apical opening, and no flange. The other cornicle, narrowed nearer

the distal end, has 10 distinct rows of reticulations, a normal opening, and a flange. In the latter aphid, one antenna is aborted at the distal end of the third segment, and the other antenna has only the proximal portion of the fourth segment; apices of both antennae are rounded.

Malformations similar to, or varying slightly from, those discussed are present in other specimens.

Species with Three Cornicles

Remaudière (1964) noted the presence of three cornicles on nymphs and adults of *Aphis* sp. near *esulae* Boerner. Of 19 specimens studied, two adults and six nymphs had three cornicles. Medler and Ghosh (1967) noted three cornicles on an alate vivipara of *Macrosiphum* sp. Russell (1975) observed three cornicles on an alate vivipara of *Aphis sambucifoliae* Fitch (Fig. 24) (prey of Asilidae, Baltimore County, Maryland, VIII-1973, A. G. Scarbrough). The additional cornicle is shorter and narrower than the other two and is nearly devoid of imbrications; the apical opening is replaced by a conical invagination and there is no flange.

Species with Four Cornicles

Remaudière (1964) found four cornicles in three nymphs of *Aphis* sp. near *esulae* Boerner, while two adults and six nymphs also in his collection had only the normal pair of cornicles. Leonard (1967) observed a pair of adventitious cornicles on an apterous vivipara of *Aphis sambucifoliae* Fitch. Russell (1975), who recorded four cornicles in an alate vivipara of *Euceraphis punctipennis* (Zetterstedt) (Fig. 25) (on *Betula* sp., Mesa, Colorado, 8-VI-1967, F. C. Hottes), stated ". . . it is the only one of 80 individuals of the lot that exhibits a duplication of cornicles." The adventitious cornicles appear to differ from the typical pair only in their smaller size. In all specimens, the additional cornicles are located on the sixth abdominal segment, posterior to, and usually slightly proximad of, the normal pair.

Branched Cornicles

Zirnits (1930) recorded conspicuous branching of cornicles in apterous viviparae of *Megoura viciae* Buckton. Perhaps the stublike extrusion we observed on the aborted cornicle of a nymph of *Acyrthosiphon kondoi* (Fig. 17) exhibits this anomaly.

Branched and supernumerary cornicles are seen less frequently than cornicles modified in size, shape and other characteristics.

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A NEW SPECIES OF *CRASPEDOXANTHA* AND A REVISED PHYLOGENY FOR THE GENUS (DIPTERA: TEPHRITIDAE)

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Abstract.—***Craspedoxantha bafut***, reared from *Vernonia calvoana* and *V. adoensis*, is newly described from specimens collected in Cameroon and Nigeria. A cladistic analysis of the 10 species of *Craspedoxantha* Bezzi with *Orellia punctata* (Schrank) as an outgroup was performed using Hennig86 (c). Using the "implicit enumeration" option of Hennig86, four trees of equal length (16 steps) were calculated from which a Nelson consensus tree was then generated. Using the successive weighting technique of Hennig86 further reduced the number of trees to two, which differed only in the sequence of Afrotropical species of the *manengubae* group. A Nelson consensus tree of these two trees is the same as the second tree. All trees that were calculated, including the Nelson trees, confirmed the validity of the two previously established species groups, *marginalis* and *manengubae*.

Key Words: *Craspedoxantha*, fruit flies, phylogeny, *Vernonia*

Freidberg (1985) recently revised *Craspedoxantha* Bezzi and included a discussion of its biology and phylogeny. His phylogeny divided the genus into two species groups: the *marginalis* group, with four Afrotropical species, and the *manengubae* group, with five species, of which three are Afrotropical and two are Oriental. The character data for the phylogeny were analyzed by hand, and the topology of the published tree was based in part on intuition.

During a recent field trip to Cameroon and Nigeria, a new species of *Craspedoxantha* was reared and collected from species of *Vernonia* (Asteraceae). Its discovery provides a good opportunity to test and refine the phylogeny of the genus with the addition of more characters and by using a computer program (Hennig86 (copyrighted), see Fitzhugh 1989 for description) for calculating and analyzing trees from the character data.

Craspedoxantha bafut
Freidberg and Mathis,
NEW SPECIES
Figs. 1–4

Diagnosis.—This species is placed unambiguously in the *manengubae* group (Freidberg 1985: 189, 202) because of its similarity to the Afrotropical congeners, *manengubae* Speiser, *yaromi* Freidberg and *vernoniae* Freidberg, of that species group. In the key to species (loc. cit.), this species runs to couplet 8, which contains *vernoniae* and *manengubae*. It differs from *vernoniae* by the yellow marginal wing band, which does not widen opposite crossvein r-m. It differs from *manengubae* by the apical blackish spot on the wing, which does not broaden in cell r4+5 and is less than ¼ as wide as the length of the apical section of vein M. The terminalia, however, are more

similar to those of *C. yaromi*, especially the aculeus (Figs. 1–2), which is only slightly more rounded and wider at the tip, the spermatheca (Fig. 3), and the epandrium (Fig. 4), which is slightly different in lateral view but indistinguishable in ventral view. *C. bafut* can otherwise be distinguished from *C. yaromi* by its larger size (length of wing: 5.5–6.5 mm versus 4.5–5 mm in *C. yaromi*), by having predominantly dark, not pale, setulae on the scutellum, by the marginal wing band not widened opposite crossvein r-m, and by the lack of yellow pattern in and around the discal cell, although a microtrichial pattern, similar to the yellow pattern usually present on the wing of *C. yaromi*, is usually present in *C. bafut*.

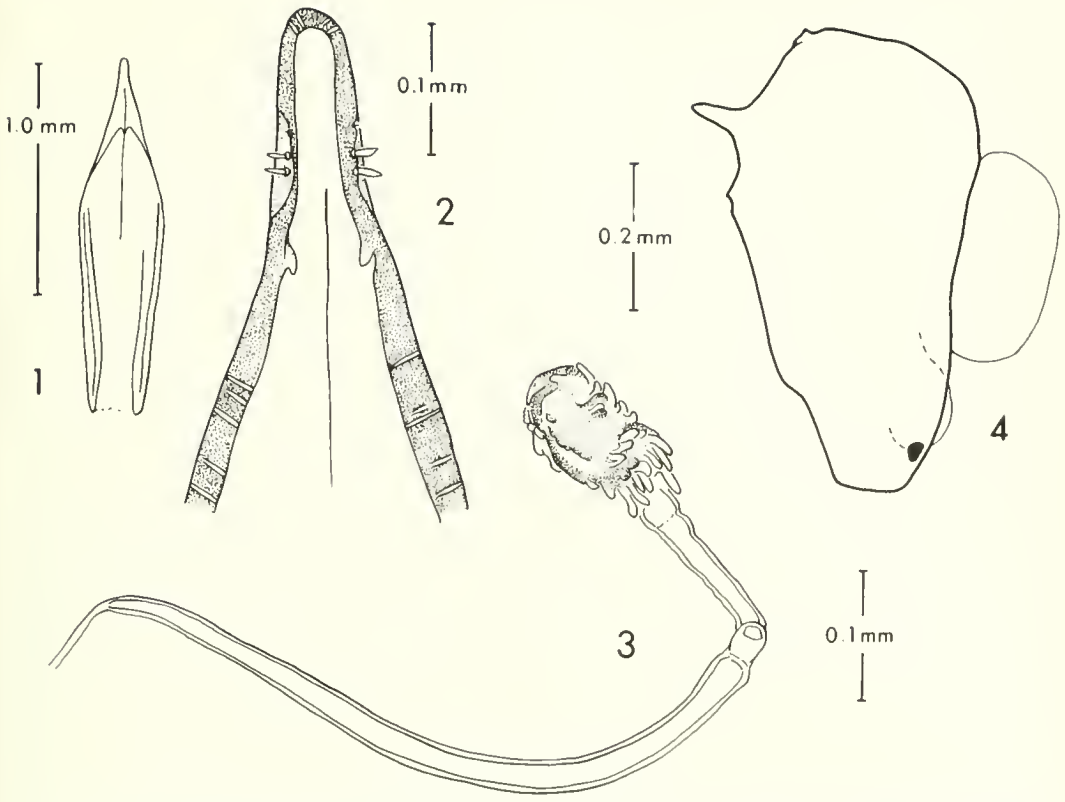
Description.—Fitting the generic description (Freidberg 1985), with the following details.

Head: Similar in shape to *C. marginalis* (Freidberg 1985, fig. 1), but with shorter 1st flagellomere, only 1.5–2 times as long as wide and 1.5 times as long as pedicel (in *C. marginalis* 2.5 times). Dull yellow, except face whitish and ventral facial margin shiny.

Thorax: Normal for genus; scutal length to width ratio = 1.1:1; dorsocentral setae aligned about midway between anterior supra-alar setae and suture; 1 anepisternal seta; dorsocentral and prescutellar black spots large; supra-alar spot and presutural spot slightly smaller than dorsocentral spot and often more elongate; scale-like setulae on scutum very dense, white or yellow, hardly extended beyond black, lyre-like pattern, which is discernable with difficulty. Scutellum unspotted, predominantly covered by blackish setulae, with yellowish setulae only near insertion of basal scutellar seta; pleura not striate; subscutellum and mediotergite brownish to blackish, densely covered by grayish-yellow microtomentum, except corners of subscutellum and ventral margin of mediotergite, which in posterior view appear less densely covered by microtomentum. Calypteres white to yellow, with or without brownish margins; halter yellow. *Legs:* Yellow, elongate; femora without distinctly dense setulae ventrally. *Wing:* Length 5.5–6.5 mm; marginal band uniformly narrow, without a bump opposite crossvein r-m; apical blackish spot evenly narrow, as wide as 1/6–1/4 of terminal section of vein M; cell cup very lightly yellow; wing with microtrichial pattern in and around cell dm similar to the yellow pattern of *C. yaromi* (Freidberg 1985, fig. 13); microtrichia lacking from apical 1/2 of cell br except near posterior part of crossvein r-m, from basal part of cell r4+5 except near posterior part of crossvein r-m, from cell bm and from base of cell dm; vein R4+5 with 2–8 setulae dorsally and ventrally at node.

Abdomen: Normal for genus; with predominantly yellow setulae, tergite 3 through last with 1 or few rows of brown setulae posteriorly; pattern of black spots reduced in ♂ to anterior band on tergite 5, which is microtomentose, matt, and a pair of small spots at posterior margin, and often entirely reduced in ♀, although in some ♀♀ a pair of small spots present at anterior margin of tergite 6 and at base of syntergosternite 7 (oviscape) and tip of syntergosternite 7 narrowly blackish; syntergosternite 7 about as long as combined length of posteriormost 4 tergites; ♂ terminalia as in Fig. 4; ♀ terminalia as in Figs. 1–3. The distiphallus is practically indistinguishable from that of *C. vernoniae* (Freidberg 1985, Fig. 29).

Type material.—*Holotype* ♀: "CAMEROON, Rt. N6 Bali-Batibo W. of Bamenda 20.XI.1987 A. FREIDBERG." The allotype ♂, and four paratypes (2 ♂, 2 ♀) have the same label data as the holotype, except the collector of one ♂ is Fini Kaplan, and one ♀ is also labeled: ex. flowerhead of *Vernonia calvoana* 23 Nov 1987. Additional paratypes are as follows: CAMEROON. Northwest Province: Rt. P16 Mbengwi 25 Km W Bamenda, 23 Nov 1987, Fini Kaplan, 1 ♀; Rt. N11, Bafut 20 Km N. Bamenda, 17-24 Nov 1987, A. Freidberg, 1 ♀. NIGERIA. Plateau State: Kurra Falls, 60 Km SE Jos, 5–7 Dec 1987, A. Freidberg, 2



Figs. 1–4. *Craspedoxantha bafut*. 1, aculeus. 2, apex of aculeus. 3, spermatheca. 4, epandrium, lateral view.

♂ 2 ♀, of which 1 ♂ 2 ♀ are also labeled: ex. flowerhead of *Vernonia adoensis*, 10 Dec 1987; Keffi, Rt. 234, 4 Dec 1987, Fini Kaplan, 1 ♂. The holotype is in excellent condition, is pinned directly, and is deposited together with most paratypes in the Zoological Museum, Tel-Aviv University. Paratypes have also been deposited in the BMNH and USNM.

Biology and host plants.—All specimens were collected or reared from *Vernonia adoensis* Sch. Bip. ex Walp. or *V. calvoana* (Hook. f.) Hook. f. (Asteraceae). The specimens from Rt. N6, between Bali and Batibo, were collected together with numerous specimens of *C. manengubae*, a species that probably also breeds in *V. calvoana*, although this latter association has not been confirmed.

Etymology.—This species is named after Bafut, a picturesque village in the highlands of Cameroon, where this species was collected. The specific epithet is a noun in apposition.

Phylogeny of *Craspedoxantha*

Freidberg (1985) briefly discussed the phylogeny of *Craspedoxantha* and noted that the genus clearly formed a monophyletic group within the tribe Terelliini. The synapomorphies that establish the monophyly of the genus are those Freidberg used to distinguish it in his key to the genera of Terelliini. With one additional character, these synapomorphies are as follows:

1. Eye is 1.5–2 times higher than long.
2. Scutum with three pairs of black spots

that are uniquely arranged as follows: at the base or immediately behind the presutural supra-alar seta and at the base of the dorsocentral and prescutellar acrostichal setae.
3. Scutellar disc with at least some blackish setulae.
4. Wing with a complete, mostly yellow costal band. The apex of the band, from vein R2+3 to slightly beyond vein M, is mostly blackish, and there are usually three, seldom two, blackish, evenly spaced spots in cell r1.

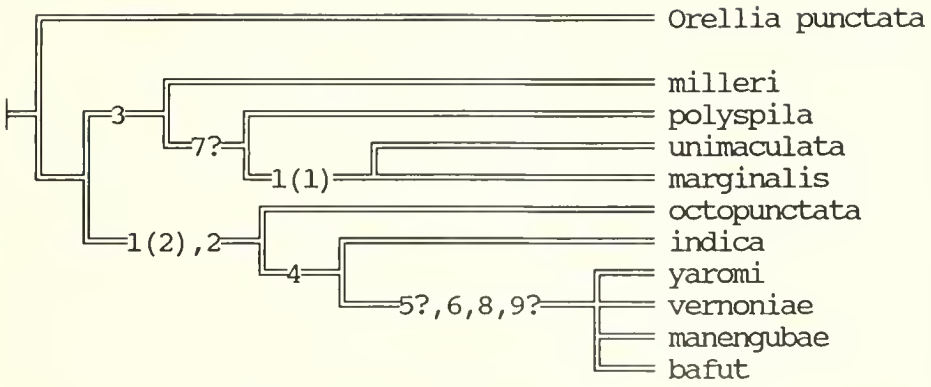
Freidberg further noted that among terelliines the closest relative of *Craspedoxantha* was probably *Orellia* Robineau-Desvoidy, especially species in the *falcata* group, which includes *punctata* (Schrank) (the type species of *Orellia*), *falcata* (Scopoli), and *distans* (Loew.) Korneev (1985) removed from *Orellia* all species except those of Freidberg's *falcata* group, thus reducing the genus to a more firmly established monophyletic group.

In the analysis to follow, *Orellia punctata*, the exemplar we chose to represent *Orellia*, was selected as the outgroup of *Craspedoxantha*. Although *O. punctata* appears to be a suitable candidate for this analysis, we are not completely satisfied with this selection. Our reservations derive from a lack of phylogenetic perspective on the tribe in general. Despite several recent publications on the taxonomy of the tribe (Freidberg 1985, Freidberg and Mathis 1986, Korneev 1982, 1985, 1987), very little has been reported on the phylogeny of the included taxa (e.g. Freidberg 1985). A better understanding of the phylogeny of the tribe and its six or seven currently recognized genera (seven in Freidberg (1985), six in Korneev (1987), who relegated *Cerajocera* Rondani to subgeneric status within the genus *Terellia* Robineau-Desvoidy) would have greatly facilitated the selection of an outgroup for *Craspedoxantha*. The main impediment to achieving a phylogeny for the tribe is our lack of knowledge about the outgroup of the Terelliini. Terelliini is now generally thought to belong in the subfamily Tephritinae, and from other studies, we suggest that *Xyphosia* Robineau-Desvoidy could possibly be its sister group, although this and other possibilities await further study and resolution.

Despite not having a well-corroborated phylogeny from which an outgroup for *Craspedoxantha* could be selected, we feel that *Orellia* ought to be considered for the following reasons. *Orellia*, as characterized by Korneev (1985) and accepted by us, shares with *Craspedoxantha* three characters that are probably synapomorphies: (1) a generally similar arrangement of black mesonotal spots, (2) a relatively short and heavily sclerotized distiphallus that lacks elongate, distal tubes (Korneev's (1985) "paired sclerites of epiduct"—this character is also shared by *Chaetorellia* Hendel, *Chaetostomella* Hendel and some *Terellia*), and (3) the host plants of *Craspedoxantha* and *Orellia* tend to be in Asteraceae other than the tribe Cardueae, a character also shared by *Neaspilota* Osten Sacken.

Nine characters were used in the phylogenetic analysis, and most of these were illustrated previously (Freidberg 1985). In accordance with standard procedures for cladistic analysis, we ordered and polarized the characters. We then coded the characters, with the most plesiomorphic states, such as those of the outgroup, as 0, and the more apomorphic states as 1 and 2. The coding we assigned to character states is given in parentheses. For purposes of clarification, we have included, as needed, an explanation of the characters in the listing as follows:

1. Scutellum with 4 (0), 2 (1), or 0 (2) black spots.
2. Anepisternal setae numbering 2 (0), or 1 (1).
3. Femora slender and lacking dense investment of setulae (0), or swollen and densely setulose ventrally (1).



Tree length 17; Consistency Index 64; Retention Index 82

Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	3	2
Consistency Index:	66	100	100	100	50	100	33	66	50
Retention Index:	83	100	100	100	75	100	50	75	50

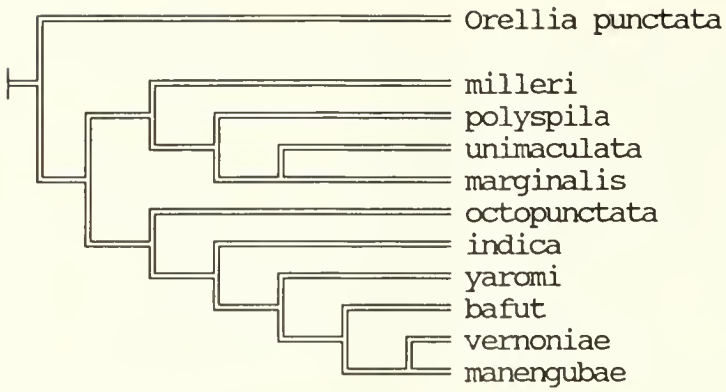
Fig. 5. Nelson consensus tree and its analysis for species of *Craspedoxantha* with *Orellia punctata* as the outgroup. A "?" denotes characters that are partially homoplasious.

4. Dorsocentral setae aligned with anterior supra-alar setae (0), or inserted more anteriorly (1).
5. Cell cup distinctly (0), or indistinctly (1) yellow.
6. Presutural black spots about as large as (0), or distinctly smaller than (1) dorsocentral spots.

Table 1. Character matrix for *Orellia punctata* and species of *Craspedoxantha*. Missing or unavailable data are indicated by a ?.

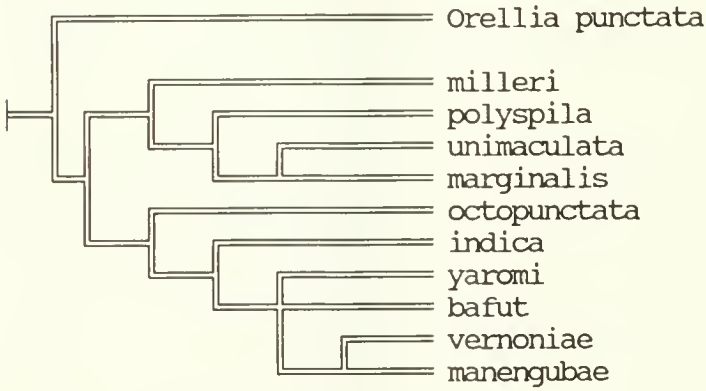
Taxon	123456789 (Characters)
Orellia punctata	000000000
C. unimaculata	1010001??
C. marginalis	101000101
C. milleri	0010000??
C. polyspila	001010100
C. octopunctata	21000000?
C. indica	210100000
C. yaromi	210111011
C. vernoniae	210111021
C. manengubae	210111121
C. bafut	210111111

7. Marginal band on the wing approaching (0) or not approaching (1) crossvein r-m. In some species of *Craspedoxantha* the marginal wing band is uniformly narrow and does not noticeably approach the junction of crossvein r-m and vein R4+5 (coded 1). In most other species the band has a small posterior bump that reaches or almost reaches this point. In *C. milleri* Freidberg and species of *Orellia* this bump is actually part of a transverse band. For all the latter taxa it was coded 0.
8. Posterior margin of the epandrium, the surface from which the cerci arise, in lateral view concave (0), straight (1) or convex (2).
9. Host plants: Host plant associations that are in part or exclusively with *Vernonia* (tribe Vernonieae) are hypothesized as the derived condition (1). We are unable to differentially treat other associations, whether they include plants of the tribe Cardueae (hosts of most Terelliini), Lac-



Tree length 88; Consistency Index 86; Retention Index 94

Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	2	2
Consistency Index:	66	100	100	100	50	100	33	100	50
Retention Index:	83	100	100	100	75	100	50	100	50



Tree length 88; Consistency Index 86; Retention Index 94

Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	2	2
Consistency Index:	66	100	100	100	50	100	33	100	50
Retention Index:	83	100	100	100	75	100	50	100	50

Figs. 6–7. Two trees calculated with the successive weighting technique and their analysis. The second Nelson consensus tree, which was calculated from these two trees, is identical with Fig. 7.

tuceae (hosts of *Orellia* species) or others and considered them all as primitive (0).

Trees were calculated from the character data using the "implicit enumeration" option of Hennig86. This option generates the most parsimonious tree(s), i.e. the tree(s) of minimal length or with fewest number of steps. Four trees of equal, minimal length (16 steps) were calculated, and a Nelson consensus tree (Fig. 5) was then generated from these four trees to demonstrate where branches and relationships are consistent (most of the lineages) or inconsistent (the

African members of the *manengubae* group). The overall consistency index for this Nelson tree is 0.64, with a "retention index" of 0.83 (formula for the "retention index" is in Fitzhugh 1989). An analysis of this tree indicates that about half of the characters (2, 3, 4 and 6) have a perfect consistency index and that the characters that are most homoplasious (as judged by the indices) are characters 5, 7 and 9. Characters 5 and 7 deal with wing pattern, a feature that is often subject to homoplasy in Tephritidae. Character 9 involves host-plant data and in addition to having some apparent homoplasy, also suffers from a lack of information for three of the species.

As more than one tree resulted from the "implicit enumeration" option, we then used the successive weighting technique (Farris 1969, Carpenter 1988) to further resolve and assist in the selection of a tree. Two trees resulted from this procedure (Figs. 6–7) and were summarized in the form of a second Nelson consensus tree (Fig. 7). The two trees differ only in the African part of the *manengubae* group, which is the clade containing *bafut, manengubae, vernoniae* and *yaromi*. Both of these trees place *manengubae* and *vernoniae* as a monophyletic group (sister species), and the other two species either form an unresolved trichotomy with this monophyletic group (Fig. 6), or have *bafut* as the sister group to *manengubae* + *vernoniae*, and *yaromi* as a sister group to the other three species (Fig. 7). The second Nelson tree was identical with the second successive weighting tree (Fig. 7). At the moment we prefer the unresolved possibility of the first Nelson consensus tree (Fig. 5) over the other trees, because we feel that the relationships between these four species are as yet unresolved.

Two characters that have not been used in the cladistic analysis, should be mentioned. The first is the superficial similarity between the wing pattern of *yaromi* and the microtrichial pattern of *bafut*, which, together with the great similarity in the terminalia of both species, may indicate sister-group relationships between these species. The second is the zoogeographical pattern of the four species, with *vernoniae* and *yaromi* apparently restricted to East Africa, and *bafut* and *manengubae* apparently restricted to West Africa. This zoogeographical pattern may indicate the actual sister-group relationships between these four species, which differs from that suggested by the previous character. Although these species are very closely related and similar, at least in the adult stage, it is possible that studies of immature stages will resolve this quadrichotomy.

It is interesting to compare the Nelson trees (Figs. 5, 7) of this study (which includes *bafut* n. sp.) with Freidberg's (1985) intuitive tree. The similarity is rather striking. The two previously established species groups (*marginalis* and *manengubae*) are as clear in all trees that were calculated using Hennig86 and the composition of the groups is the same. There are, however, two discrepancies. In the *marginalis* group, *milleri* is placed by Hennig86 as a sister species to the other species of this group; whereas in the intuitive tree it is the sister species to *polyspila* Bezzi only. In the *manengubae* group, *octopunctata* is placed as a sister species to the other species of this group; whereas in the intuitive tree it is the sister species to *indica* Zaka-ur-Rab only. These discrepancies are mainly the result of previously underestimating single characters, such as the wing pattern of *milleri*, which differs markedly from other patterns of its species group, and using zoogeographical considerations that were not used in the present analysis. *C. indica* and *octopunctata* were considered sister species in the intuitive tree because, in addition to overall morphological resemblance, they are the only Oriental congeners, a fact that was given more weight than some morphological evidence.

In summary, the use of Hennig86 or similar computerized algorithms is strongly rec-

ommended mainly because of their objectivity and their ability to analyze large numbers of taxa and characters quickly. In addition, a prerequisite to using Hennig86 is the preparation of a well-documented character matrix, which undoubtedly improves the thoroughness of revisionary work.

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METHODS FOR IDENTIFICATION OF *ANASTREPHA* LARVAE (DIPTERA: TEPHRITIDAE), AND KEY TO 13 SPECIES

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Abstract.—Detailed methods are provided for observing useful characters to distinguish among species of *Anastrepha* fruit flies in their immature stages. Additionally, a key is provided to third instar larvae of 13 species: *A. bistrigata* Bezzi, *distincta* Greene, *fraterculus* (Wiedemann), *grandis* (Macquart), *interrupta* Stone, *leptozona* Hendel, *limae* Stone, *ludens* (Loew), *obliqua* (Macquart), *pallens* Coquillett, *serpentina* (Wiedemann), *striata* Schiner and *suspensa* (Loew). There is considerable overlap in many character states among species. Discriminant analysis is necessary to distinguish among species in some couplets.

Key Words: *Anastrepha*, fruit flies, larvae, discriminant analysis

Anastrepha is a New World genus of fruit flies (Diptera: Tephritidae) comprising about 180 valid species (Norrbom and Kim 1988). Several species are major fruit pests in the American tropics and subtropics. Descriptions are available for immature stages of only 15 species, and several of these are very incomplete. The paucity of taxonomic information makes it extremely difficult to identify the larvae of *Anastrepha* (as well as those of most other fruit flies). This is especially problematical because fruits infested with larvae usually are encountered in the absence of associated adults, as is the case of most interceptions of Tephritidae at U.S. ports of entry (APHIS 1987).

Published keys or descriptive works which specifically attempt to discriminate among larvae of two or more *Anastrepha* species include Greene (1929), Phillips (1946), Berg (1979), Heppner (1984), Steck and Wharton (1988), Steck and Malavasi (1988) and Carroll and Wharton (1989). Twelve species are included in these works, but not all of them simultaneously. Berg's key (1979) is the most inclusive and treats those six species considered to be the most serious pests (*fraterculus* (Wiedemann), *ludens* (Loew), *obliqua* (Macquart), *serpentina* (Wiedemann), *striata* Schiner, and *suspensa* (Loew). Unfortunately, some of the characters used in Berg's key are very difficult to interpret. Also, the natural variability within species is such that the key often leads to an incorrect identification.

In this paper, we incorporate additional characters not previously utilized. Since the natural variability of larval characters is so poorly documented, especially among geographical regions, we are careful to note the source and sample sizes of all the material utilized to generate the key. We have ad-

dressed the problem of variation by examining specimens from more than one locality to the extent that material was available.

The economically most important species are all included, as well as several other available species whose identities were certain. Thus, the usefulness of various larval characters could be assessed across a broad taxonomic range within this large genus. The 13 species treated here represent six different species groups within the genus (Norrbom and Kim 1988). Among species classified in the same group, the amount of overlap in character states is expectedly high. For some couplets it is necessary to employ discriminant analysis to determine the species to which a particular specimen belongs.

Materials and Methods

Specimens from which the key was developed are listed below. Accurate association of larvae with their identifiable adult forms was a critical objective of this study. Identity of larvae cannot be presumed if they are taken from naturally infested fruits, since even an individual fruit may be multiply infested by more than one species. Most museum specimens are not explicitly associated with reared adults from the same collection; thus, their identity must be considered cautiously. Many larvae used in this study were bred in the laboratory from known adults. Others were taken from naturally infested fruits from which numerous adult specimens of exclusively one species were reared. Exceptions are noted below. Specimen collectors' names are given in parentheses after the collection date. Local names for host fruits are given in parentheses after their scientific names. Asterisks denote specimens used to generate linear discriminant functions. Voucher specimens of all larvae and associated adults are housed in the collections of the U.S. National Museum of Natural History, Smithsonian Institution (USNM) and/or the Department of Entomology, Texas A&M University as TAMU voucher numbers 213, 214, 219, 220, 222, 223, 225, 226 and 227.

A. bistrigata Bezzi—BRAZIL: São Paulo, Universidade de São Paulo, XI-1986 (Steck, Malavasi); 23* + 7 specimens from a laboratory culture on *Psidium guajava* L. (guava) initiated with adults reared from guava, Campinas, S.P. (See Steck and Malavasi 1988.)

A. distincta Greene—VENEZUELA: Merida, Merida, V-1988 (Steck, Norrbom); 5 specimens from *Inga* sp. BRAZIL: Bahia, Cruz das Almas, VI-1988 (Steck, Conceição); 5 specimens from *Inga* sp. MEXICO: Chiapas, Tapachula vicinity, Obregon, III-1986 (Carroll); 10 specimens from *Inga* (larval identity presumed from host relationship). HONDURAS: E.A.P., 30 km s.e. of Tegulcigalpa, V-1985 (Sequiera); 10 specimens from *Inga* (larval identity presumed from host relationship).

A. fraterculus (Wiedemann)—BRAZIL: Saõ Paulo, Itaquera, XI-1986 (Steck, Malavasi); 25* specimens from *Eugenia brasiliensis* Lam. (grumichama); larval identity based on numerous previous rearings from the same trees and from which only *fraterculus* adults emerged (A. Malavasi, personal communication). BRAZIL: São Paulo, Universidade de São Paulo, XI-1986 (Steck, Malavasi); 5 specimens from culture on artificial medium initiated with adults from São Paulo state. BRAZIL: Bahia, Santo Amaro, VI-1988 (Steck, Conceição); 5 specimens from guava. MEXICO: Chiapas, Tapachula, Metapa, III-1986 (Carroll); 15* specimens from culture on guava initiated with adults from Tapachula area. COSTA RICA: Puntarenas, Dominical, IV-1986 (Steck, Valerio); 10* specimens from *Terminalia catappa* L. (almendron). VENEZUELA: Merida, Merida area, V–VI-1988 (Steck, Norrbom); 3 specimens from *Rubus glaucus* Benth. (mora), 3 specimens from *Syzygium jambos* L. Alston (pomarrosa) and 3 specimens from *Coffea arabica* L. (café). VENEZUELA: Dto. Federal, Las Caracas,

V-1988 (Rosales); 3 specimens from *T. catappa.*

A. grandis (Macquart)—BRAZIL: São Paulo, Universidade de São Paulo, XI-1986 (Steck, Malavasi); 18 specimens from culture on *Cucurbita maxima* Duch. and 5 specimens from culture on *Cucumis melo* L. (melon) initiated with adults reared from *C. maxima* at São Roque, S.P. ARGENTINA: 11 specimens from USNM, preserved in alcohol and bearing the following label: "*Anastrepha grandis* (Macq.) Pumpkin Argentina. 1-4-37 Houston Tex.-2003 Lot. 37-521." (See Steck and Wharton 1988.)

A. interrupta Stone—USNM: 18 specimens preserved in alcohol bearing the following label: U.S.A. "*Anastrepha interrupta* Homestead, Fla. 3.i.1951 *Schoepfia chrysophylloides* berries; 51-997 SPBFLA 109425." (See Steck and Wharton 1988.)

A. leptozona Hendel—MEXICO: Chiapas, Tapachula vicinity, Huehuetan. III-1986 (Carroll); 19 specimens from *Micropholis mexicana* (Gilly) (baricoco). (Larvae of *A. serpentina* occurred in low frequency in same collection, but were readily distinguishable.)

A. limae Stone—USNM: 31 specimens preserved in alcohol bearing the following label: "PANAMA: Capira 19–20.x.1935 J. Zetek 3552 reared ex *Passiflora quadrangularis.*" (See Steck and Wharton 1988.)

A. ludens (Loew)—MEXICO: Chiapas, Tapachula, Metapa, IV-1986 (Carroll); 15 specimens from culture on *Mangifera indica* L. (mango) initiated with adults reared from mango in Tapachula area. U.S.A.: Texas, Texas A&M University. IV-1984 (Carroll); 15 specimens from culture on artificial medium. (See Carroll and Wharton 1989.)

A. obliqua (Macquart)—MEXICO: Chiapas, Tapachula, Metapa, IV-1986 (Carroll); 20* specimens from culture on mango initiated with adults reared from *Spondias* sp. (jobo) in Tapachula area. COSTA RICA: Alajuela, F. Baudrit Expt. Stn., IV-1986 (Steck, Valerio); 9* specimens from mango. VENEZUELA: Merida, Hwy 7 × Pueblo Nuevo road, VI-1988 (Steck, Norrbom, Holmquist); 5 specimens from mango. BRAZIL: Bahia, Cruz das Almas area, VI-1988 (Steck, Conceição); 2 specimens from *Averrhoa carambola* L. (carambola), 2 specimens from *Spondias purpurpea* L. (caja) and 2 specimens from mango.

A. pallens Coquillet—USNM: 10 specimens preserved in alcohol bearing the following labels: "*Pseudodacus pallens* (Coq.) / *A. pallens* / laboratory collection Coma berries *Pseudodacus pallens* Coq. lot no. 35-19611 FHB / GVH #35."

A. serpentina (Wiedemann)—MEXICO: Chiapas, Tapachula, Metapa, III-1986 (Carroll); 20 specimens from culture on *Manilkara zapota* (L.) P. Royen (chico zapote) initiated with adults from *M. zapota, Pouteria sapota* (Jacq.) Moore and Stearn (mamey) and *Chrysophyllum cainito* L. (caimito) from Tapachula area. MEXICO: Veracruz, Los Tuxtlas Biol. Stn., VII-1984 (Steck); 11 specimens from *P. sapota.* VENEZUELA: Aragua, Maracay, V-1988 (Steck, Norrbom, Rosales); 5 specimens from *M. zapota* (nispero). BRAZIL: São Paulo, São Sebastião, VI-1988 (Amaral); 5 specimens from *M. zapota* (abrico). *A. striata* Schiner—MEXICO: Chiapas, Tapachula, Metapa, IV-1986 (Carroll); 20* specimens from culture on guava initiated with adults reared from guava in Tapachula area. COSTA RICA: Cartago, Tres Equis, Hwy 10 between Turrialba and Siquirres, 3-IV-1986 (Steck, Carlson, Valerio); 10* specimens from guava. VENEZUELA: Merida, Merida, V-1988, (Steck, Norrbom, Holmquist); 5 specimens from guava. VENEZUELA: Miranda, Guatopo National Park, VI-1988 (Condon); 5 specimens from guava.

A. suspensa (Loew)—U.S.A.: Florida, Homestead, TREC-IFAS, I-1985 (Baranowski); 30* specimens from culture on artificial medium initiated with adults from southern Florida.

In developing the key, complete measurements were taken on all specimens as in Steck and Wharton (1988). Those characters newly used in this key mostly concern the presence or absence of dorsal spinules on the various segments, and quantitative counts and measurements on the posterior spiracular processes. For convenience, some of the measurement procedures are repeated here as they relate specifically to the use of the key. Only features visible with a dissecting or compound microscope were examined. Terminology follows Teskey (1981).

Oral ridge (ORL) counts and determination of anal lobe shape are taken from whole specimens. Specimens are removed from alcohol and propped in an appropriate position on an alcohol-dampened wad of cotton in a small watchglass. The alcohol evaporates off the surface after a minute or two, and the oral ridges (Fig. 1) become clearly separable and countable. Use of a strong, fluorescent light is recommended; use of an incandescent light requires careful adjustment of the lighting angle. A minimum of 80× magnification is necessary for accurate counts on most specimens. Oral ridges are counted along the inner margin adjacent to the oral opening. The terminal upper and lower oral ridges are reduced in size and often difficult to see. The shape of the anal lobes is also best determined just after the alcohol dries off the surface of the whole specimen. (Their shape usually will be still apparent after slide-mounting.) In some species the lobes are almost always obviously bilobed (e.g. *ludens, serpentina*; Figs. 3, 4); or obviously entire (e.g. *suspensa, obliqua*; Fig. 6). In other species, such as *striata* and *distincta*, the lobes may be wrinkled or finely grooved, and thus indeterminate in this respect (Fig. 5). These latter are keyed both ways at the corresponding couplets.

Anterior spiracular tubules (ANS) are also counted on whole specimens. If the spiracles are not well exposed on the whole specimen, they become so after the specimen is treated in sodium hydroxide (NaOH).

Specimens are not perfectly symmetrical; numbers of oral ridges and anterior spiracular tubules frequently are unequal on left and right sides. Count data used in the key are the average of the two sides rounded upwards; e.g. a specimen with 10 oral ridges on one side and 11 on the other would be counted as 11 (Fig. 1). (Measurements entered into discriminant analysis, however, were not rounded.) If one anal lobe is bilobed and the other entire, the specimen is considered to be bilobed.

Dorsal spinules occur in broken, parallel rows. They usually are apparent at 80× magnification with good fluorescent lighting and best seen from a dorsolateral angle. Rows are counted on the dorsum, defined to be that surface bounded by a pair of imaginary lines drawn lengthwise between the anterior spiracle and posterior spiracle on each side (Fig. 2). Many specimens have rows of dorsal spinules interrupted by a broad, bare hiatus across the medial third of the dorsum. If rows are not visible on whole specimens, one should re-check slide-mounted specimens at 100× magnification on a compound microscope. For purposes of orientation, dorsal spinules on the second thoracic segment (T2) are those immediately posterior to the insertion of the anterior spiracles.

Specimens are slide-mounted for all remaining observations. The body is slit lengthwise along one side from just below an anterior spiracle to just above the anal lobes. Specimens are then left in 10% NaOH overnight at room temperature (or about 1 hr at 60°C). Afterwards, internal tissues are easily cleared away. The cephalopharyngeal skeleton (CPS) is gently separated from the cuticle and mounted laterally as normally figured (e.g. Steck and Wharton 1988). The cuticle is mounted flat in glycerol (or permanently mounted in Hoyer's medium or Euparal). It helps to cut small notches in the

cuticle around the posterior spiracles and anal lobes, and between the anterior spiracles so the entire specimen will lie flat (see Fig. 7). Thus mounted, rows of dorsal spinules can be counted readily.

Measurements on the posterior spiracular openings (PSO) and posterior spiracular processes, SP-I and SP-IV (Fig. 8) are made at 400× magnification using an ocular micrometer. Use of Nomarski optics provides a 3-dimensional perspective and facilitates counting of trunks and tips of spiracular processes. Measurements and counts are usually made on only one side, right or left, choosing whichever side is best positioned. PSO are measured to the outside edges of the heavily sclerotized rimae; values used in the key for length (LTH) and width (WTH) are the averages of the dorsal and ventral openings. Likewise, number of tips (TIP) and trunks (TRK) is the average of SP-I and SP-IV. The number of tips usually is readily countable. Determination of the number of trunks as clearly separate insertions into the cuticle is sometimes difficult due to orientation or crowding. In practice, when the insertion points are obscured, any branch seen as separate beyond about the basal 10% is counted as a trunk. The basal width (BAS) is the distance between outermost trunks at their insertion points; again, the average of SP-I and SP-IV is used.

Throughout development of the key we tried to use ratios of measurements on related structures (e.g. basal width of SP-I and SP-IV to length of PSO) as key characters to avoid biases resulting from unusually large or small specimens (related perhaps to type of host fruit utilized). The user of this key will note, however, that numerous couplets rely on absolute measurements, e.g. length of PSO, distal width of anterior spiracles, etc. For these latter characters, ratios did not prove useful in distinguishing among species, whereas the absolute measurements did.

Very little has been published on intraspecific geographical variation in larval characters. Some of the complexity of this key arises from such variation. It is possible that other populations besides those sampled here will fall outside the key ranges. In our *ludens*, for example, the range of lengths of PSO for Weslaco specimens did not overlap with the range for specimens from Tapachula. (The key does not use this particular character in arriving at an identification of *ludens*.) Larvae of *A. fraterculus* may present an especially thorny problem, since there are long-standing, unresolved questions about the occurrence of cryptic species in different geographical regions. Larvae of other species also display non-overlapping states for various characters among assorted populations. We foresee more such problems arising as other geographical regions are sampled.

The key works strictly on the basis of morphological characters. When information on host fruit and geographic origin of specimens are available, the task of identification is considerably simplified. Table 1 summarizes host and distribution information for the 13 species included in the key.

Within-species variability was extensive, and few, if any, single characters could reliably be used to diagnose species. An adequate number of specimens was examined in most cases to allow us to delimit ranges in which most key character states fell. We aimed for a key which would allow accurate identification for 95% or more of all specimens examined. Thus, we did not include numerous additional couplets to accommodate those specimens which displayed extreme character state values. In view of the difficulties, we would consider any determination based on a single specimen to be suspect. When several specimens of a collection are examined, the likelihood of a correct determination is greatly increased.

In some cases, there was so much overlap in key character states between species, that a simple bifurcating key became unmanageable. This was true for *striata/bistrigata*

Table 1. Host plants and geographical distributions of *Anastrepha* species.

Species	Host Plants	Distribution
bistrigata	*Psidium*	southern Brazil, northern Peru
distincta	*Inga*	southern Texas to South America
fraterculus	numerous	southern Texas to South America
grandis	cucurbits	South America, Panama
interrupta	*Schoepfia*	southern Florida, Bahamas
leptozona	*Chrysophyllum, Pouteria, Micropholis*	Central and South America
limae	*Passiflora*	Venezuela, Panama, Texas
ludens	numerous	southern Texas to Costa Rica
obliqua	numerous	Mexico to South America, Caribbean
pallens	*Bumelia*	Texas to Honduras
serpentina	numerous	southern Texas to South America
striata	numerous	Mexico to South America
suspensa	numerous	Greater Antilles, Bahamas, southern Florida

and *fraterculus/obliqua/suspensa*. Multivariate statistics were employed to discriminate among species at the corresponding couplets. The data were analyzed using SAS (1988). Observations of potentially useful characters were first subjected to univariate analysis to check for normality; non-normally distributed measurements were transformed as needed. Characters were then subjected to stepwise discriminant analysis (Lachenbruch 1975). The significance level specified to enter and to keep a character was 0.05. Those characters retained as useful discriminating factors in the stepwise analysis were incorporated into discriminant analysis to develop a model for actually identifying specimens. Classification results were cross-validated by a jackknifing technique. The original models were also retested using sets of new observations on additional specimens. Specimens marked with asterisks in the preceding collections list were used to develop the discriminant models.

Results of stepwise discriminant analysis are presented in Table 2, in which relevant statistics are shown for only those characters which contributed significantly to the discriminant function. The complete sets of characters used for each stepwise discriminant analysis are as follows (significant variables are indicated by asterisks): Couplet 4′—ANS*, TRK*, $\log_{10}$(BAS)*, ORL, LTH, TIP, squareroot(WTH), RTO1 (=LTH/WTH), $\log_{10}$(RTO2) (where RTO2 = TIP/TRK), and $\log_{10}$(RTO3) (where RTO3 = BAS/LTH); couplet 14′—ORL*, ANS*, LTH*, $\log_{10}$(BAS)*, $\log_{10}$(RTO2)*, TIP, TRK, RTO1, $\log_{10}$(RTO3), squareroot(WTH); couplet 14′A and couplet 14′B—same characters as 14′, but with different significant variables; couplet 15—$\log_{10}$(BAS)*, $\log_{10}$(RTO2)*, LTH, TIP, TRK, RTO1, $\log_{10}$(RTO3), squareroot(WTH). Thus, for example, at couplet 4′, ten characters (some transformed) were analysed for discriminating *striata* and *bistrigata*. Only three characters (ANS, TRK and $\log_{10}$(BAS), indicated with asterisks, contributed significantly to the discriminant function.

The discriminant models presented in Table 3 can be used to identify individual specimens which key to the corresponding couplet. The character values for a given specimen are substituted into the equation. Whether the equation yields a positive or negative value (except couplet 14; see below) indicates to which species the specimen is most likely to belong. Consider, for example, a hypothetical specimen which keys to couplet 4′ and has 13.5 anterior spiracles (13 on one side, 14 on the other; note that values used in discriminant functions are

Table 2. Stepwise discriminant analysis results.

Step	Variable* Enter	Remove	Partial R^2	F	Prob > F
Couplet 4′: *striata* vs *bistrigata*					
1	$\log_{10}$BAS	—	0.388	28.49	0.0001
2	ANS	—	0.175	9.32	0.0038
3	TRK	—	0.167	8.64	0.0053
Couplet 14′: *suspensa* vs *fraterculus* vs *obliqua*					
1	LTH	—	0.548	49.64	0.0001
2	$\log_{10}$BAS	—	0.391	25.99	0.0001
3	ORL	—	0.294	16.68	0.0001
4	$\log_{10}$RTO2	—	0.315	18.14	0.0001
5	ANS	—	0.120	5.32	0.0068
Couplet 14′A: *fraterculus* vs *obliqua*					
1	LTH	—	0.478	58.62	0.0001
2	$\log_{10}$BAS	—	0.242	20.11	0.0001
3	ANS	—	0.110	7.68	0.0074
Couplet 14′B: *suspensa* vs *obliqua*					
1	LTH	—	0.598	65.57	0.0001
2	TIP	—	0.244	13.91	0.0006
3	ORL	—	0.137	6.69	0.0133
4	ANS	—	0.141	6.74	0.0130
Couplet 15: *fraterculus* vs *suspensa*					
1	TIP	—	0.482	62.35	0.0001
2	$\log_{10}$BAS	—	0.159	12.52	0.0007
3	$\log_{10}$RTO2	—	0.113	8.28	0.0054
4	—	TIP	0.012	0.81	0.3729

* Abbreviations: ANS, number tubules on anterior spiracles; BAS, basal width of posterior spiracular processes; LTH, length posterior spiracular opening; ORL, number oral ridges; TIP, number tips on posterior spiracular processes; TRK, number trunks on posterior spiracular processes; WTH, width posterior spiracular opening; RTO1, ratio LTH to WTH; RTO2, ratio TIP to TRK; RTO3, ratio BAS to LTH. All measurements in μm.

not rounded), 18 trunks, and a PSP basal width of 46.8 μm ($\log_{10} = 1.67$). When these values are substituted into the couplet 4′ equation, the calculation yields a value of +2.79. A positive result indicates that the specimen is *striata*; and, using the cross-validation error rate from Table 4, one would conclude that the likelihood of error is 0.231. In the case of couplet 14, a simple positive or negative result is not possible since three species are involved. A discriminant function is provided for each of the three species. Character values for an unknown specimen are substituted into each of the three equations; whichever yields the highest value (C) indicates the most likely identification. Because the natural distributions of *fraterculus* and *suspensa* do not overlap, couplets 14′ and 15 might not represent likely sets of alternatives. Therefore, we also provide discriminant analyses for the pairwise comparisons of *fraterculus* and *obliqua* (couplet 14′A), which overlap throughout mainland Central and South America, and *obliqua* and *suspensa* (couplet 14′B) which overlap in the Caribbean (Table 3).

The performance of the classification rule was examined using three error rates (Table 4): (1) the apparent error rate (errors in classifying the original specimens using the classification rule calculated from measurements on those specimens); (2) the error rate from cross-validation using a jackknifing technique; and (3) the error rate in classifying a different set of test specimens. The apparent error rate underestimates the true error rate, although this bias is reduced if the sample size is large enough. The cross-validation method using the jackknife technique is almost unbiased (Lachenbruch 1975, Panel . . . 1989). The jackknife method gives an assessment of the true probability of misclassification of additional specimens taken from the original populations. The error rate from the test data set indicates the robustness of the classification rule when applied to other populations of specimens. The classification results indicated by the apparent and cross-validation errors for each couplet of Table 4 are very similar indicating that sample sizes were adequate for developing each of the discriminant models. The model for couplet 4′ performed poorly for the test specimens of *bistrigata*, probably due to the fact that the few test specimens available were in poor condition. Also, models 14′, 14′B and 15 fared relatively poorly for *suspensa* test specimens. This indicates that the data base for *sus-*

Table 3. Linear discriminant functions.

Couplet 4':

$23.5(\log_{10}BAS) - 0.75(ANS) - 0.63(TRK) - 15.00 > 0$ *striata*
< 0 *bistrigata*

Couplet 14':

fraterculus $186.07(\log_{10}BAS) + 13.01(ORL) + 39.58(\log_{10}RTO2) + 8.63(ANS) + 1.10(LTH) - 294.42 = C_f$
suspensa $151.06(\log_{10}BAS) + 17.23(ORL) - 5.62(\log_{10}RTO2) + 8.51(ANS) + 1.25(LTH) - 285.19 = C_s$
obliqua $161.23(\log_{10}BAS) + 14.17(ORL) + 27.96(\log_{10}RTO2) + 9.77(ANS) + 1.58(LTH) - 326.32 = C_o$

Couplet 14'A:

$22.70(\log_{10}BAS) - 0.45(LTH) - 0.99(ANS) + 24.00 > 0$ *fraterculus*
< 0 *obliqua*

Couplet 14'B:

$1.40(ANS) + 0.60(T1P) + 0.24(LTH) - 2.45(ORL) - 30.93 > 0$ *obliqua*
< 0 *suspensa*

Couplet 15:

$24.20(\log_{10}BAS) + 26.67(\log_{10}RTO2) - 40.52 > 0$ *fraterculus*
< 0 *suspensa*

pensa should be augmented with specimens from additional populations.

As noted previously, it has not been possible to construct a key to accommodate all the variability observed in our samples. However, the accuracy of the key is very high. The percentage of study material which keyed correctly (*before discriminant analysis) was as follows (sample sizes for each species in parentheses): **bistrigata* (30)/*striata* (40)—100%, *distincta* (30)—97%, **fraterculus* (72)/*obliqua* (40)/*suspensa* (40)—100%, *grandis* (34)—100%, *interrupta* (18)—100%, *leptozona* (19)—95%, *limae* (31)—100%, *ludens* (30)—100%, *pallens* (10)—100% and *serpentina* (41)—98%.

The generic description and diagnosis presented below are based on published descriptions by other authors (especially Kandybina 1977) and on additional unpublished observations of our own. With the exception of holarctic species of *Rhagoletis*,

Table 4. Error rates of classification by discriminant analysis.

	Species	Apparent Error	Crossvalidation Error	Test Error (sample size)
Couplet 4':	*striata*	0.192	0.231	0.125 (n = 8)
	bistrigata	0.046	0.091	0.500 (n = 4)
Couplet14':	*fraterculus*	0.026	0.026	0.222 (n = 9)
	suspensa	0.158	0.158	0.429 (n = 7)
	obliqua	0.148	0.148	0.167 (n = 6)
Couplet 14'A: Larvae originating in Central or South America				
	fraterculus	0.025	0.025	0.214 (n = 14)
	obliqua	0.143	0.143	0.182 (n = 11)
Couplet 14'B: Larvae originating in Caribbean				
	obliqua	0.074	0.074	0.000 (n = 7)
	suspensa	0.000	0.000	0.286 (n = 7)
Couplet 15:	*fraterculus*	0.136	0.136	0.111 (n = 9)
	suspensa	0.172	0.172	0.333 (n = 9)

the larvae of relatively few species of fruit-infesting Tephritidae have been adequately described.

Larvae of numerous Diptera families may be found in fruits (Keifer 1930), though only a few of these would be found in ripe, healthy fruits suitable for human consumption. Besides Tephritidae, only a few species of Lonchaeidae are likely to be encountered. These are readily distinguished from tephritids by the appearance of the posterior spiracles. In lonchaeids they comprise a pair of prominent stumps, round, black, and heavily sclerotized, projecting from the caudal segment; rimae of spiracular openings are at nearly right angles. In tephritid fruit flies, the spiracular openings comprise a pair of three elongate slits, nearly flush with the body surface; their rimae are sclerotized and golden-brown, and their long axes are roughly parallel. Among Tephritidae, other fruit-infesting genera which may be encountered in the Neotropics and subtropics include endemic *Rhagoletis* and *Toxotrypana* and introduced species of *Ceratitis* and *Dacus*. *Rhagoletis* generally are distinctive in possessing prominent, chitinized teeth or "stomal guards" adjacent to the oral opening and strongly developed intermediate and ventral tubercles on the caudal segment (see Phillips 1946, Kandybina 1977), neither of which are seen in *Anastrepha*. *Toxotrypana* is largely restricted to papaya, larvae are very large, and all caudal sensilla are greatly reduced (see Heppner 1986). *Ceratitis* and *Dacus* both may be recognized by the presence on the caudal segment of a distinct crescent-shaped ridge connecting, or just dorsad of, sensilla I1 and I2 (see Heppner 1985, Elson-Harris 1988) and conspicuous dental sclerites (see Exley 1955). The caudal ridge is lacking and dental sclerites usually are not seen in *Anastrepha* larvae. The diagnostic and key characters are for third instars only, and cannot be applied to earlier instars. Sections I to III of the key will eliminate most specimens for which the key is not intended.

Anastrepha Generic Description (third instar)

Body elongate, 4–7 times longer than wide, pointed anteriorly. Integument thin, smooth, colorless. Spinules separate, conical, in short, staggered rows (occasionally flat, blunt, basally connected in short rows); occurring in discrete fusiform areas ventrally on all abdominal segments; also dorsally in bands on T1, T2, usually T3, present or absent on abdominal segments. Antennal and maxillary sensory organs on well-developed cephalic lobes above mouthhooks. Antennal sensory organ appearing 2-segmented with basal sclerotized, cylindrical collar and apical hemispherical to conical sense organ. Maxillary sensory organ cylindrical, truncate, apically bearing peg-shaped sensoria. Oral ridges 7–30 per side, well developed. Stomal organ minute cluster of sensilla borne distally on large, simple, oblong lobe anterior to mandible. Sclerotized stomal guards absent. Cephalopharyngeal skeleton with clearly separate sclerites as follows: Mandible falciform (occasionally uncurved and blunt), single-toothed, length to height ratio (lateral view) about 1.0–1.5, heavily sclerotized; dental sclerite apparently lacking or small and inconspicuous; epipharyngeal and labial sclerites present; hypopharyngeal sclerite in dorsal view H-shaped, width at bridge about equal to length (ratio, 0.75–1.25), and length in lateral view about twice height, anterior forks heavily sclerotized; parastomal bar long and thin, usually bent medially, 0.75–1.0 times length of hypopharyngeal sclerite; anterior sclerite irregularly developed and shaped; dorsal cornua narrowly connected at dorsal bridge; ventral cornu trough-shaped, with 7 pharyngeal ridges. Anterior spiracle with distinct, cylindrical trunk; sharply flared and bilobed apically with numerous (9–37) tubules. Caudal segment more or less smooth and rounded; intermediate sensilla I1 and I2 on relatively developed tubercles; remaining sensilla (D1, D2, I3, L1, V1–V3) on weak

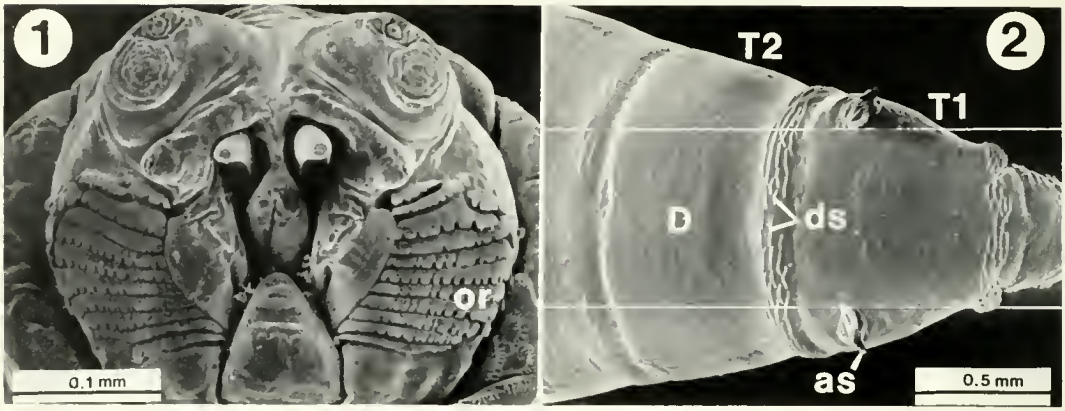


Fig. 1. Oral ridges (or), *A. suspensa.*

Fig. 2. Dorsal surface of *A. limae.* Abbreviations: as, anterior spiracle; D, dorsum bounded by imaginary lines drawn between anterior spiracles and posterior spiracles; ds, dorsal spinules in 3–4 rows on segment T2 (note hiatus in rows of spinules across mid-dorsum of segment T3); T1 and T2, first and second thoracic segments.

or undeveloped tubercles. Posterior spiracles located above horizontal midline; with three slits having well-developed rimae and trabeculae. Anal lobes entire or bifid; encircled by spinules.

Key to *Anastrepha* larvae (third instar)

I

1. Posterior spiracles prominently raised from the body surface; or most body segments with conspicuous setae or processes; or posterior spiracular openings sinuous . . . . *not* Tephritidae
1′. Posterior spiracles nearly flush with body surface; tubercles, if present, on caudal segment only; posterior spiracular slits elongate or oval II

II

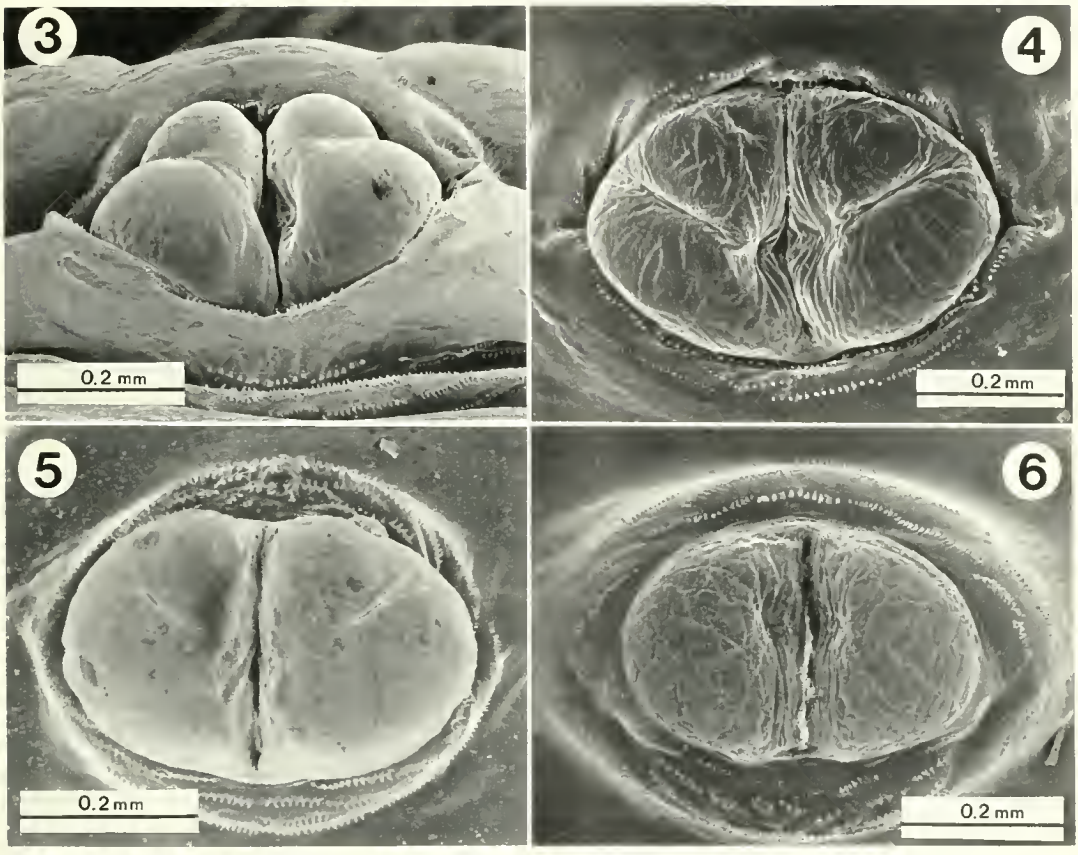
1. With prominent chitinized teeth (stomal guards) adjacent to oral opening, and strongly developed tubercles on caudal segment; or, with crescent-shaped ridge between sensilla I1 and I2 on caudal segment and conspicuous dental sclerite; or, larva taken from papaya, very large (more than 12 mm long), caudal tubercles lacking and caudal sensilla all very reduced . . . . . *not Anastrepha*
1′. Lacking stomal guards; caudal tubercles at most moderately developed; lacking crescent ridge on caudal segment; dental sclerite lacking or inconspicuous; not normally attacking papaya; at least caudal sensilla I1 and I2 conspicuous III

III

1. Anterior spiracle absent, and posterior spiracle with only 2 openings; and/or, mandible with well-developed subapical tooth, and posterior spiracular openings short (less than 55 μm) and oval; and body short and thin (less than about 6.0 mm long and 1.0 mm diameter) . . . . . *not* 3rd instar
1′. Anterior spiracle present; posterior spiracle with 3 elongate openings at least 65 μm long; mandible without subapical tooth; body length and diameter greater than about 6.0 mm by 1.0 mm IV

IV. *Anastrepha,* third instar

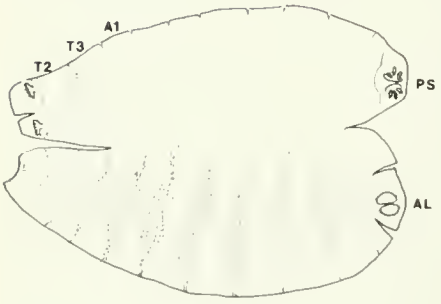
1. Dorsal spinules present on two or more abdominal segments 2
1′. Dorsal spinules present on A1, but not beyond 5
1″. Dorsal spinules absent on all abdominal segments 7
2. Dorsal spinules separate, conical; in fewer than 5–6 rows on T2 and T3 (except *limae*). Posterior spiracular processes SP-I and SP-IV with average of 6 or more trunks and bristle length ⅓ or more times length of spiracular opening 3
2′. Dorsal spinules connected basally in flat, sawtooth pattern, blunt-tipped; in 8 or more



Figs. 3–4. Bifid anal lobes, *A. serpentina.*
Fig. 5. Indeterminate, grooved anal lobes, *A. distincta.*
Fig. 6. Entire anal lobes, *A. fraterculus.*

rows on T2 and T3, at least 3 rows on A1 to A4, 1–4 rows (often with medial hiatus) on A5. SP-I and SP-IV with average of 5 or fewer trunks, and bristle length about ⅛ times length of posterior spiracular opening ..... *pallens*

3. Anterior spiracle with 12–23 tubules; distal width 0.19–0.37 mm 4
3′. Anterior spiracle with 28–37 tubules; distal width 0.43–0.61 mm ..... *grandis*
4. SP-I and SP-IV with average of 8–12 trunks and 12–21 tips; basal width 12–19 μm, 0.1–0.2 times length of spiracular opening. Dorsal spinules absent on A3 ..... *limae* (part)
4′. SP-I and SP-IV with average of 13–23 trunks and 23–49 tips; basal width 19–67 μm, 0.2–0.5 times length of spiracular opening. Dorsal spinules usually present on A3 ..... *striata* ..... *bistrigata* ..... (See Table 3, couplet 4′)
5. Dorsal spinules weakly developed on A1, in only 1 row, usually with broad medial hiatus; T2 with 2–4 rows; T3 with 1–3 rows, often with medial hiatus 6
5′. Dorsal spinules well-developed on A1, in 2 or more rows, without medial hiatus; both T2 and T3 with 5–6 rows ..... *limae* (part)
6. Anterior spiracle with 14–22 tubules. Posterior spiracular opening 94–130 μm long. SP-I and SP-IV with average of 7–13 trunks and 17–28 tips ..... *ludens* (part)*
6′. Anterior spiracle with 10–13 tubules. Posterior spiracular opening 72–84 μm long. SP-I and SP-IV with average of 4–7 trunks and 5–11 tips ..... *interrupta* (part)*
7. Oral ridges 7–11 8
7′. Oral ridges 12 or more 16
8. Anterior spiracle with 15 or more tubules 9
8′. Anterior spiracle with 9–14 tubules 14
9. Anal lobe bifid 10
9′. Anal lobe entire 11
10. Posterior spiracular opening 74–96 μm long. SP-I and SP-IV with average basal width of



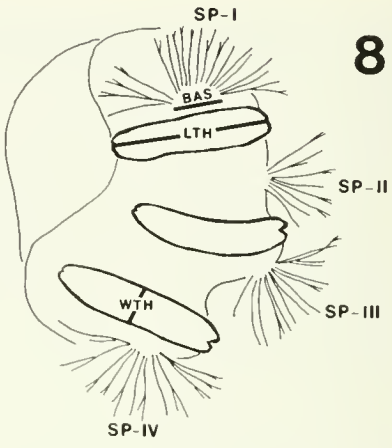


Fig. 7. Slide-mounted cuticle: AL, anal lobes; PS, posterior spiracles; T2 and T3, second and third thoracic segments; A1, first abdominal segment.

Fig. 8. Posterior spiracle (right side): SP-I to SP-IV, dorsal to ventral spiracular processes; BAS, basal width of spiracular process; LTH, spiracular opening length; WTH, spiracular opening width.

12–22 μm, 0.1–0.2 times length of spiracular opening; average of 7–11 trunks ..... *serpentina* (part)

10′. Posterior spiracular opening 103–122 μm long. SP-I and SP-IV with average basal width of 29–58 μm, 0.3–0.5 times length of spiracular opening; average of 10–17 trunks ..... *distincta* (part)

11. Anterior spiracle with 17 or more tubules .. 12

11′. Anterior spiracle with 9–16 tubules 13

12. SP-I and SP-IV with average basal width of 29–58 μm, 0.3–0.5 times length of spiracular opening ..... *distincta* (part)

12′. SP-I and SP-IV with average basal width of 14–20 μm, 0.1–0.2 times length of spiracular opening ..... *leptozona* (part)

13. SP-I and SP-IV with average of 10–17 trunks and 24–37 tips. Anterior spiracle distal width 198–273 μm ..... *obliqua* (part)

13′. SP-I and SP-IV with average of 6–10 trunks and 13–23 tips. Anterior spiracle distal width 260–335 μm ..... *leptozona* (part)

14. Anal lobe bifid 15

14′. Anal lobe entire ..... *suspensa* (part) ..... *fraterculus* (part) ..... *obliqua* (part) ..... (See Table 3, couplets 14′, 14′A, 14′B)

15. Anterior spiracle with 9–13 tubules, and SP-I and SP-IV with average of 11 or more trunks ..... *fraterculus* (part) ..... *suspensa* (part) ..... (See Table 3, couplet 15)

15′. Anterior spiracle with 13–14 tubules, and SP-I and SP-IV with average of 11 or fewer trunks ..... *serpentina* (part)

16. Anterior spiracle with 15 or more tubules .. 17

16′. Anterior spiracle with 9–14 tubules 20

17. SP-I and SP-IV with average basal width of 10–24 μm, 0.1–0.3 times length of spiracular opening 18

17′. SP-I and SP-IV with average basal width of 24–65 μm, 0.3–0.6 times length of spiracular opening ..... *distincta* (part)*

18. Anal lobe bifid 19

18′. Anal lobe entire ..... *leptozona* (part)

19. Dorsal spinules present on T3 (rows often with medial hiatus). Posterior spiracular opening 40–54 μm long ..... *ludens* (part)

19′. Dorsal spinules absent on T3. Posterior spiracular opening 31–40 μm long ..... *serpentina* (part)

20. Dorsal spinules present on T3 (rows may have medial hiatus) 21

20′. Dorsal spinules absent on T3 .. *serpentina* (part)

21. SP-I and SP-IV with average of 15 or more tips and 7 or more trunks. Up to 16 oral ridges 22

21′. SP-I and SP-IV with average of 5–11 tips and 7 or fewer trunks. Up to 20 oral ridges ..... *interrupta* (part)*

22. Anal lobe bifid. Anterior spiracle distal width 260–347 μm. Up to 16 oral ridges ..... *ludens* (part)*

22′. Anal lobe entire. Anterior spiracle distal width 161–248 μm. Up to 12 oral ridges ..... *suspensa* (part)*

* indicates that 10% or fewer of the individuals of a given species key to the corresponding couplet.

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A NEW SPECIES OF THE MINUTE PREDACEOUS MIDGE GENUS *NANNOHELEA* FROM SRI LANKA (DIPTERA: CERATOPOGONIDAE)

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Abstract.—*Nannohelea tamil,* a new species of minute predaceous midge from Sri Lanka is described and illustrated. A key to the extant species of *Nannohelea* is provided.

Key Words: Diptera, Ceratopogonidae, *Nannohelea,* predaceous midges, new species, Sri Lanka, Oriental

Grogan and Wirth (1980) proposed the minute predaceous midge genus *Nannohelea* composed of 3 species: *bourioni* (Clastrier) (1961), as type-species, from France and Algeria (Palearctic); *fuscipennis* (Tokunaga) (1964), from New Guinea and Malaysia (Oriental and Australasian); and *clastrieri* Grogan and Wirth (1980), from Columbia (Neotropical). Recently, Szadziewski (1988) described 2 new species from Eocene Baltic amber (ca. 40 million years old), suggested that the genus is of Laurasian origin, and that it probably migrated to South America during the Tertiary.

We recently obtained 4 specimens of *Nannohelea* collected by Ginter Ekis in Sri Lanka during 1973 that represent a new species apparently most closely related to *N. fuscipennis.* In addition to describing this new species, we also present a key to the extant species of *Nannohelea.*

For an explanation of general ceratopogonid terminology, see Downes and Wirth (1981); for special terms dealing with predaceous midges in the tribe Ceratopogonini, see Wirth and Grogan (1988). The types of this new species will be deposited in the National Museum of Natural History, Washington, D.C. (USNM).

KEY TO THE EXTANT SPECIES OF *NANNOHELEA*

1. Females 2
– Males 4
2. Anal lobe of wing poorly developed, with fringe of 6–10 short capitate setae; small species, wing length 0.68–0.74 mm; Palearctic Region . . . . . *bourioni* (Clastrier)
Anal lobe of wing well developed, with fringe of normal slender setae; very small species, wing length 0.47–0.49 mm; Oriental and Australasian Regions 3
3. Eyes contiguous; wing with vein R2+3 much shorter than r-m crossvein, radial cell narrow, cubital fork obsolete on distal ⅔ . . . . . *fuscipennis* (Tokunaga)
– Eyes narrowly separated; wing with vein R2+3 as long or longer than r-m crossvein, radial cell rounded, cubital fork obsolete only at extreme tip at wing margin . . . . . *tamil,* new species
4. Flagellum with 8 flagellomeres; small species, wing length 0.50–0.55 mm . . . . . *bourioni* (Clastrier)
Flagellum with 7 flagellomeres; very small species, wing length 0.37–0.43 mm 5
5. Eyes contiguous; flagellum with only distal 2 flagellomeres elongated, antennal ratio 0.82–0.85 . . . . . *fuscipennis* (Tokunaga)
– Eyes separated; flagellum with distal 3 flagellomeres elongated, antennal ratio 1.38 or greater 6
6. Aedeagus with long slender basal arms; flagellum with last flagellomere bearing a single apical trichoid sensilla, antennal ratio 1.38–1.39 . . . . . *tamil,* new species

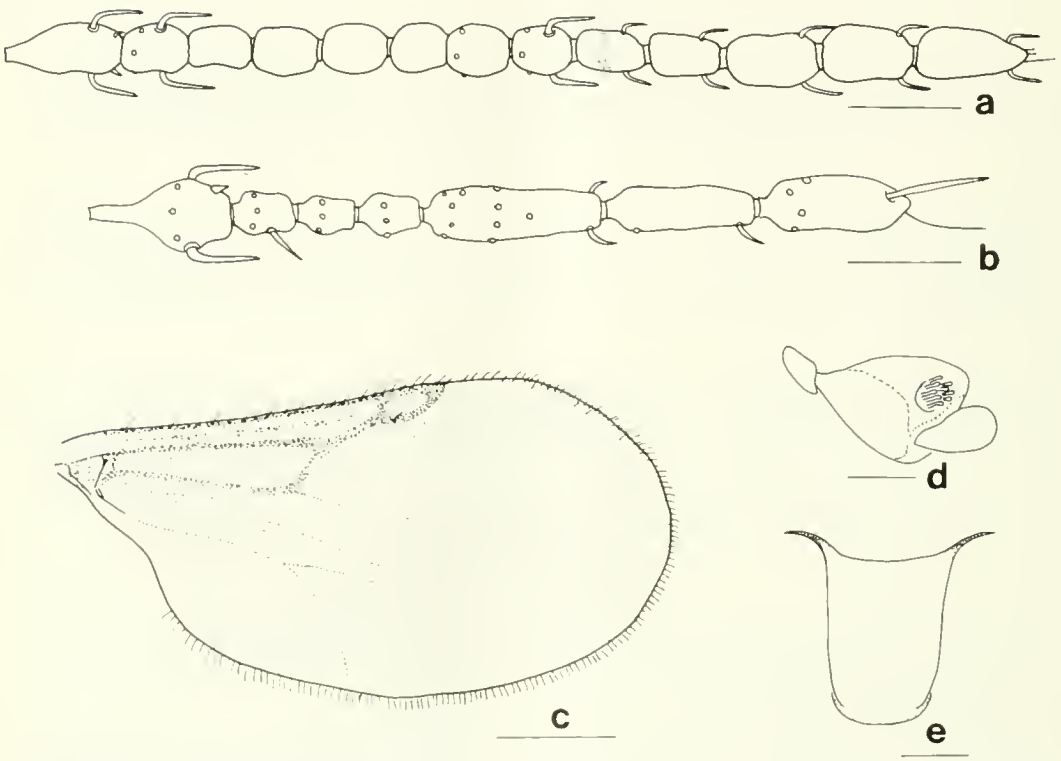

Fig. 1. *Nannohelea tamil*. a, female flagellum; b, male flagellum; c, female wing; d, male palpus; e, aedeagus. Scale bars = 0.03 mm (a–b), 0.1 mm (c), 0.01 mm (d–e).

– Aedeagus with short stout basal arms; flagellum with last flagellomere bearing 2 trichoid sensilla, antennal ratio 1.93 ..... *clastrieri*, Grogan and Wirth

Nannohelea tamil Grogan and Wirth, New Species
(Fig. 1)

Diagnosis.—Differs from its congeners by the following combination of characters: very small size (female wing length 0.47 mm, male wing length 0.41 mm); wing with well developed anal lobe, vein R2+3 in nearly a straight line with and as long or longer than r-m crossvein, radial cell rounded; eyes separated; male aedeagus with long slender basal arms and rounded tip.

Holotype female.—*Head:* Dark brown. Eyes pubescent, narrowly separated. Antenna with dark brown pedicel; flagellum (Fig. 1a) light brown with darker brown bands on midportion of distal 5 flagellomeres, proximal 8 flagellomeres bearing a pair of stout subapical trichoid sensilla bent at 90° angle near base, flagellomere 1 with a pair of apical sensilla basiconica, distal 5 flagellomeres with subapical pair of sensilla basiconica that are also bent at base; lengths of flagellomeres in proportion of 21-11-12-11-11-11-11-12-13-13-18-18-20; antennal ratio 0.82. Clypeus with 2–3 pairs of submarginal setae. Palpus similar to that of male (Fig. 1c) but somewhat disoriented due to mounting; segment 2 very broad with large deep sensory pit bearing capitate sensilla. Mandible very small with 4 small curved teeth.

Thorax: Dark brown. Scutum without anterior spine or humeral pits, covered with short fine pubescence and a few large setae; scutellum with 4 bristles; postscutellum

highly produced. Legs light brown; femora moderately slender, unarmed, stoutest on fore leg; tibiae slender, unarmed, stoutest on hind leg, hind tibia with comb of 6 setae and bifurcated or trifurcated spur; tarsi with apical spines on tarsomeres 1–3 of mid leg only, tarsomere 1 of hind leg with well developed palisade setae, tarsomeres 4 cylindrical, tarsomeres 5 slender and bearing small equal sized simple claws. Wing (Fig. 1c) infuscated dark brown, membrane covered with microtrichia, macrotrichia confined to anterior margin at tip and a few on radial sector; fringe moderately long, extending from base of costa to halfway up anal lobe; anal lobe well developed; a rounded radial cell present; r-m crossvein rather long and set at an oblique angle; vein R2+3 nearly in line with and as long as r-m crossvein; vein M1 straight, obsolete only near wing margin, M2 absent; cubitus forking at level of r-m crossvein, obsolete only near wing margin; anal veins absent; costal ratio 0.59; wing length 0.47 mm, breadth 0.27 mm. Halter light brown.

Abdomen: Brown. Two large spermathecae, partially collapsed, apparently ovoid with long slender necks, one of which is 0.06 mm in length including the neck.

Allotype male.—Smaller but similar to holotype female with the following notable differences: Antennal flagellum (Fig. 1b) reduced to only 7 flagellomeres; flagellomere 1 with only a single apical sensilla basiconica, flagellomere 2 with only a single straight trichoid sensilla, flagellomere 5 with a pair and flagellomere 6 with a single sensilla basiconica, flagellomere 7 with a single long straight sensilla trichodea; lengths of flagellomeres in proportion of 31-15-13-13-40-30-29; antennal ratio 1.38. Palpus (Fig. 1d) 3 segmented; segments in proportion of 12-33-19; palpal ratio 1.32. Mandible vestigial, without teeth. Wing length 0.41 mm, breadth 0.24 mm; costal ratio 0.59. Genitalia very small, distorted due to mounting; sternite 9 very short, caudal margin straight; tergite 9 apparently very short, extending only ½ the length of gonocoxite. Gonocoxite straight, very short; gonostylus longer than gonocoxite, tapering slightly distally to a narrow rounded tip. Aedeagus highly distorted, a reconstruction of that of paratype shown in Fig. 1e; basal arm slender; distal portion with rounded tip. Parameres not discernible in holotype, but visible in paratype as a slender bridge that connects the bases of the gonocoxites.

Type material.—Holotype female, allotype male, one female and one male paratype labeled "SRI LANKA: Rat. Dist., Gilimale Lumber Mill, 7 VIII 1973, 115 feet, Ginter Ekis" (USNM).

Distribution.—Sri Lanka.

Etymology.—The specific epithet, *tamil*, is a reference to the small Dravidian people that inhabit the forests of Sri Lanka.

Remarks.—*Nannohelea fuscipennis* (Tokunaga) most closely resembles this new species but differs from it in having contiguous eyes, a wing with a smaller radial cell and the cubitus vein obsolete basally and on the distal ⅔, a more slender 2nd palpal segment, male antenna with only distal 2 flagellomeres elongated and the aedeagus is pointed apically. *Nannohelea clastrieri* Grogan and Wirth, known only from a single male from Colombia, differs in having an aedeagus with short basal arms and the last flagellomere has 2 apical sensilla trichodea. *Nannohelea bourioni* (Clastrier) from France and Algeria differs by being a larger species (female wing length 0.68–0.74 mm; male wing length 0.50–0.55 mm), the wing of the female has a poorly developed anal lobe bearing capitate setae, and the male flagellum has 8 flagellomeres. The 2 species of *Nannohelea* that were recently described by Szadziewski (1988) from Eocene Baltic amber differ from all extant species in having a 4 segmented palpus.

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HOST SPECIFICITY AND ESTABLISHMENT OF *APHTHONA FLAVA* GUILL. (CHRYSOMELIDAE), A BIOLOGICAL CONTROL AGENT FOR LEAFY SPURGE (*EUPHORBIA ESULA* L.) IN THE UNITED STATES

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Abstract.—The potential host plant range of the European flea beetle *Aphthona flava*, a candidate biological control agent for leafy spurge, *E. esula*, was evaluated. Fewer than 19 (none of which are rare or legally protected) of the 113 *Euphorbia* species native to the U.S. appear to be potential host plants for *A. flava*. Releases of *A. flava* were made in Montana (1985–1987), North Dakota (1985) and Idaho (1986). Establishment occurred in four of the eight Montana sites, and at the North Dakota site. *Aphthona flava*, which increased to 31 beetles/m^2 at one Montana site in 1988, is part of a complex of insects being introduced in an attempt to control leafy spurge, a serious weed of Great Plains rangelands.

Key Words: biological control of weeds, flea beetle, Great Plains, rangeland, weed

Leafy spurge (*Euphorbia esula* L.) is a deep rooted perennial herb native to Europe and Asia, which has become one of the most serious weeds of rangelands in the Great Plains region of North America (Lacey et al. 1985, Watson 1985). Cattle, one of the primary products of the Great Plains, will not eat the plant nor much of the palatable forage growing near it (Messersmith and Lym 1983). Chemical control is usually not economical on the low value land that leafy spurge infests. For this reason, and since leafy spurge was not known to be a problem in its native Eurasian range, a biological control program was begun in the early 1960s by Agriculture Canada (Harris 1984).

The USDA's Agricultural Research Service joined the effort to discover, test and introduce insects of spurge in the mid 1970s (Pemberton 1985). These programs have resulted in the introduction of the following complex of European *Euphorbia* feeding insects to the United States: a foliage and flower feeding moth (*Hyles euphorbiae* L., Sphingidae), a root feeding moth (*Chamaesphecia tenthrediniformis* (Den. and Schif.), Aegeriidae), a stem boring beetle (*Oberea erythrocephala* (Schrank), Cerambycidae), a shoot-tip gall midge *Spurgia capitigena* Gagne, Cecidomyidae) and four root feeding flea beetles *Aphthona flava* Guill., *A. cyparissiae* (Koch), *A. czwalinae* Weise and *A. nigriscutis* Foudras (Chrysomelidae) (Pemberton 1985, Rees et al. 1986, Pemberton and Rees, unpublished data).

Aphthona flava is one of a complex of 40 *Aphthona* spp. recorded to feed on *Euphorbia* spp. in Europe (Harris et al. 1985) and Asia (Pemberton and Wang 1989). Like other *Aphthona* species that feed on *Euphorbia* species, the adults of *A. flava* feed

on leaves and flower bracts, and the larvae feed upon the root hairs and roots. *A. flava* has one generation per year. The adults usually emerge in June, feed and lay eggs for several months before dying. The mature larvae overwinter and pupate in late spring or early summer. This flea beetle is native to Europe, from northern Italy, east and north through Yugoslavia, Hungary, Czechoslovakia, Bulgaria, Rumania and Russia (Sommer and Maw 1982). It has been recorded from *Euphorbia cyparissias* L., *E. esula* L., *E. seguieriana* Necker and *E. pannonica* Host. (Kuntze 1930, Sommer and Maw 1982, Harris et al. 1985).

Aphthona flava was evaluated as a candidate biological control agent for leafy spurge by Sommer and Maw (1982), who found that the beetle's potential host range would be limited to species of *Euphorbia*. Based on these data, *A. flava* was introduced to Alberta and Saskatchewan, Canada (McClay and Harris 1984). Before *A. flava* could be introduced into the United States, additional host specificity testing was needed to better define the beetle's potential host range within the genus *Euphorbia*.

Host Specificity Testing

The United States has 113 native species of *Euphoria* (sensu lato), including two rare species (*E. garberi* Engelm. ex Chapm. and *E. deltoidea* Engelm. ex. Chapm.) that are legally protected and nine other rare species that are under review for protected status (U.S. Dept. Agric. 1982, U.S. Dept. Inter. 1980 and 1983, Pemberton 1985). It is not possible to predict from the European host plant records which of these North American *Euphorbia* species could become host plants of *A. flava*, because most American *Euphorbia* species belong to subgenera (*Agaloma* and *Chamaesyce*) that are not represented in the European flora. *Aphthona flava*, from *E. esula* near Pisa, Italy, was tested against ten North American *Euphorbia* species in the USDA–ARS quarantine in Albany, California, during 1984 and 1985 (Pemberton, unpublished data). The *Euphorbia* species used in the testing included representatives of the subgenera that occur in North America[1] and species that are rare, weedy, ornamental, or sympatric with leafy spurge.

Host plant suitability was studied by placing adult beetles with test plant bouquets or potted plants to measure adult feeding and longevity; and by transferring eggs or first instar larvae to potted test plants to see which plants could support full larval development (to the third instar).

Table 1 summarizes the results of these studies. None of the tested members of the subgenera *Chamaesyce* (3 of the 57 U.S. species) or *Agaloma* (2 of the 26 U.S. species) were suitable hosts by any of the criteria measured. All six tested species of the subgenus *Esula* (21 U.S. species) were accepted as adult food. Three of these (*E. incisa* Engelm., *E. robusta* (Engelm.) Small and *E. palmeri* Engelm.) supported adult longevity for more than two months. These three species and *E. spatulata* Lam. supported full larval development. Significantly, neither *E. purpurea* (Raf.) Fernald or *E. telephiodes* Chapm., both rare subgenus *Esula* species under review for protected status, appeared to be suitable hosts, since no larval development took place on these plants.

From these data, we predict that some portion of the remaining 19 subgenus *Esula* species could be potential host plants for *A. flava*, if the beetles were to spread through the United States. If *A. flava* becomes established throughout the North American range of leafy spurge, eight subgenus *Esula* species, which are roughly sympatric with leafy spurge, might become host plants for the beetle. The most sympatric of these is *E. robusta*, a Rocky Mountain species (U.S. Dept. Agric. 1982), which was an acceptable laboratory host plant in the testing. *Eu-*

[1] No species of the small subgenus *Poinsettia* (3 U.S. species) were used, since the two species tested by Sommer and Maw (1982) did not support development.

Table 1. Summary of *Aphthona flava* host plant specificity testing on native North American *Euphorbia* species.[a]

Test Plant Species	Subgenus	% of Plants Accepted for Adult Feeding	% of Adults Living 2 Months or Longer	% of Plants Supporting Larval 3rd Instar
Euphoria esula	*Esula*	100 (10/10)	86 (19/20)	90 (27/30)
Euphorbia incisa	*Esula*	100 (10/10)	63 (10/16)	90 (9/10)
Euphorbia palmeri	*Esula*	80 (8/10)	53 (8/15)	88 (7/8)
Euphorbia robusta	*Esula*	80 (8/10)	63 (10/16)	80 (8/10)
Euphorbia spatulata	*Esula*	—	5 (1/20)	20 (2/10)[d]
Euphorbia purpurea[b]	*Esula*	30 (3/10)	0 (0/16)	0 (0/10)
Euphorbia telephiodes[b]	*Esula*	60 (6/10)	0 (0/16)	0 (0/10)
Euphorbia maculata	*Chamaesyce*	0 (0/10)	0 (0/16)	0 (0/10)
Euphorbia supina	*Chamaesyce*	0 (0/10)	0 (0/16)	0 (0/10)
Euphorbia serpyllifolia	*Chamaesyce*	0 (0/10)	0 (0/16)	0 (0/10)
Euphorbia corollata	*Agaloma*	10 (10/10)	0 (0/16)	0
Euphorbia marginata[c]	*Agaloma*	0	0	0
Euphorbia heterophylla[c]	*Poinsettia*	0	0	0

[a] From Pemberton unpublished data 1984–85.
[b] Rare species.
[c] Tested by Sommer and Maw 1982.
[d] Many small plants were in each pot, single plants are probably too small to support larval development.

phorbia incisa and *E. palmeri*, which were also acceptable laboratory hosts, are southwestern species (U.S. Dept. Agric. 1982) that may have some contact with leafy spurge in Nevada or northern Arizona. The other acceptable laboratory host plant, *E. spatulata*, is a small annual that ranges throughout much of the United States (U.S. Dept Agric. 1982). Larval development of *A. flava* occurred in 20% of the pots densely planted with *E. spatulata*; single plants may be too small to support complete larval development. The other sympatric species are: *E. brachycera* Engelm., a southwestern perennial, and three annuals: *E. commutata* Engelm. from the east and south central U.S., *E. lurida* Engelm. from the northeast, and *E. crenulata* Engelm). of the Pacific states.

Since relatively few of the 113 *Euphorbia* species native to the U.S. appeared to be potential hosts of *A. flava*, a petition (Pemberton unpubl. report) for its release was made to the Federal Working Group of Biological Control of Weeds. Approval for release was received in 1985 and releases began the same year.

Release and Establishment

All *A. flava* beetles intended for release were collected from leafy spurge populations in the Pisa area of northern Italy by M. Stazi and M. Cristofaro (U.S. Dept. Agric.–ARS Biological Control Laboratory, Rome). Each collection was sent to the U.S. Dept. Agric.–ARS Biological Control of Weeds Quarantine in Albany, California. In the quarantine, a small number (usually ca. 5%) of the beetles were killed and sent to Consulting Diagnostic Service (Berkeley, Calif.) to check for internal pathogens. None were found. A small number of specimens were also sent to R. White (U.S. Dept. Agric.–ARS U.S. National Museum, Washington) to confirm their identity. The remaining beetles were paired and placed on bouquets of leafy spurge to observe feeding and record oviposition. Beetles that fed and laid eggs normally were sent to the field for release.

There was a very high mortality (80–95%) experienced by overwintering larvae in laboratory cultures which significantly reduced

Table 2. Releases and Establishment of *Aphthona flava*.

Site	Number Released	Date	Number of Adults Recovered	Date
Montana[a]				
North Bozeman (Gallatin Co.)	59	16 July 1985	no recovery (site sprayed 1986)	
Reed Point (Stillwater Co.)	50	31 July 1985	2 2	9 June 1987 10 June 1988
Columbus Island (Sweetgrass Co.)	57	31 July 1985	1	9 June 1987
Glacier National Park (Flathead Co.)	150	2 Aug 1985	no recovery to date	
Gallatin River (Gallatin Co.)	46	4 Aug 1985	no recovery to date	
Lyman Creek-Shade (Gallatin Co.)	106	25 June 1986	× 31/m²	4 Aug 1988
Clyde Park (Park Co.)	240	10 July 1986	no recovery to date	
Lyman Creek-Sun (Gallatin Co.)	2077 in 6 releases	9 July–6 Aug 1987	51/278 sweeps	22 July 1988
Idaho[b]				
Featherville (Elmore Co.)	200	8 July 1986	no recovery to date	
Rathdrum (Kootenai Co.)	210	24 July 1986	no recovery to date	
North Dakota[c]				
Bald Hill Dam (Barnes Co.)	260 in 2 releases	11–23 July 1986	× 7.5/m² × 14/m²	July–Aug 1987 July–Aug 1988

[a] Montana releases made primarily be N. Rees and R. Pemberton.
[b] Idaho releases made by J. McCaffrey, University of Idaho at Moscow.
[c] North Dakota release made by R. Carlson, North Dakota State University at Fargo.

the number of beetles for field colonization. Consequently foreign field collected beetles, instead of laboratory reared material, were released. Since no parasites or pathogens had been found in Italian *A. flava* populations (although many are known from other areas (Sommer and Maw 1982)), release of field collected material from this area appeared to have few risks, and seemed justified to try to establish the beetle in the U.S. Direct release of foreign collected material in the U.S., as a normal mode of operation, is unwise, since pathogens and parasites, which could negate successful biological control programs, could easily be introduced. In 1988, after the releases of *A. flava* from Italy reported here were completed, a pathogenic microsporidian, *Nosema* sp., and a lethal parasitic mite, *Trombidium susteri* Feider, were found to be associated with *Aphthona* spp. collections, originating from Austria, that were intended for release in the U.S. (G. Johnson, El Cerrito, Calif., pers. comm.).

Aphthona flava was released in Montana from 1985 to 1987, and in North Dakota and Idaho in 1986 (Table 2). The seven Montana releases, east of the Continental Divide, were made by the authors (primarily NER) assisted by N. Poritz. The Glacier Park release was made by D. Lang (National Park Service, West Glacier). All of the Montana sites had dense infestations of leafy spurge, estimated to constitute more than 50% of the above ground dry weight annual plant production.

Brief descriptions of the Montana sites are as follows: The North Bozeman site (altitude ca. 1600 m) is 3.2 km northeast of Bozeman and south of the Bridger Moun-

tains in Gallatin County. It consists of an open, south facing slope cut by a shallow valley, which in addition to dense leafy spurge, had *Rosa* sp., and mixed annual grasses. This site had a history of herbicide spraying (Tordon and 2–4 D ester) for leafy spurge control and was, unfortunately, sprayed in 1986, the year following the release.

The Reed Point site (altitude ca. 1200 m) is 9.3 km east of Reed Point in Stillwater County. The spurge infestation is on the south bank of the Yellowstone River, between the river and highway I-90. The site is a level terrace that has been used as a cattle pasture. The vegetation, except for *Salix* along the river, was weedy, including *Iva xanthifolia* Pursh. and *Asclepias speciosa* Torr., in addition to the leafy spurge. Part of the site was plowed in 1986, the year after the release.

The Columbus Island Site (altitude ca. 1100 m) is a rock and sand island, of ca. 2 hectares, in the Yellowstone River adjacent to the town of Columbus in Sweetgrass County. The dominant plants are *Populus deltoides* Marsh, *Salix* and *Rosa* spp. The leafy spurge density was 48 stems/m^2 in 1983. Goats have been used extensively at this site in an attempt to control leafy spurge.

The Gallatin River site (altitude ca. 1600 m) is 9.6 km east of Bozeman in Gallatin County. The site lies on the east side of the Gallatin River and is dominated by *Populus angustifolia* James, leafy spurge and the exotic tansy (*Tanacetum vulgare* L.). Leafy spurge had a density of 129 stems/m^2 in 1987. The site has had periodic grazing.

The Glacier Park site (altitude ca. 980 m) is located at Big Prairie on the east bank of the Flathead River in the western sector of the Park. In addition to large growths of spurge, this natural prairie has a mixture of small herbs and grasses with patches of introduced *Linaria vulgaris* L. The site had been plowed historically, but has been free of agriculture for many years. The Park Service has used mowing, burning, and a limited amount of plowing to try to control the leafy spurge at this site.

The Lyman Creek Shade site (altitude ca. 1600 m) is located on the northern bank of Lyman Creek on the southern slopes of the Bridger Mountains ca. 8 km north of Bozeman in Gallatin County. Leafy spurge grows in a 50 m^2 opening, surrounded by Douglas fir (*Pseudotsuga menziesii* (Mirbel Franco), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and *Prunus virginiana* L. Both Lyman Creek sites are on the City of Bozeman Water Company land and have had no grazing or chemical use for many years.

The Clyde Park (altitude ca. 1600 m) is 5.6 km northeast of Clyde Park and south of the Crazy Mountains in Park County. The site consists of a level pasture, with *Artemisia* spp., *Lupinus* sp. and some grass, and a 30 m long 45° slope running from the pasture to a *Populus trichocarpa* T. & G. dominated riparian community. The beetles were released on the slope, which was densely covered by leafy spurge. The site, particularly the level portion, has been grazed and treated with herbicides to try to control leafy spurge.

The Lyman Creek Sun site is an open, south facing hillside located ca. 200 m down stream from the Lyman Creek Shade site. The open infested hillside (ca. 1400 m^2) is surrounded by Douglas fir and aspen (*Populus tremuloides* Michx. On the hillside are *Geranium viscosissimum* Fish. & Mey. and species of *Equisetum, Balsamorhiza, Artemisia, Rosa* and *Symphoricarpos*. In 1988, leafy spurge accounted for 77.5% (SD ± 21.8) of the above ground dry weight plant biomass on the hillside. The $\bar{x}$ leafy spurge density was 216.5 g/m^2 (SD ± 99.42).

The North Dakota release was made by R. Carlson assisted by D. Mundal, North Dakota State University at Fargo. The release site is at Bald Hill Dam in Barnes County. The site is adjacent to the reservoir and has zones of prairie and woodland consisting of planted shelter belt. The leafy spurge density was 133.4 stems/m^2 in 1986.

The Idaho releases were made by J. McCaffrey of the University of Idaho at Moscow. The Rathdrum site (altitude ca. 760 m) is located in Kootenai County in northern Idaho. Leafy spurge accounted for more than 50% of the annual production at this site, which in addition to spurge, had mixed annual grasses.

The Featherville site (altitude ca. 1500 m) is in Elmore County in southern Idaho. The site is a disturbed sagebrush-grass community with an estimated spurge density of 50 stems/m^2 in about a one hectare infestation.

The Montana releases at North Bozeman, Reed Point, Columbus and Lyman Creek Shade were made in 3 m × 3 m plastic screen cages to concentrate the beetles and possibly aid their establishment. The remaining Montana releases were made in the open. The Idaho releases were made within one m^2 cages and in the open near the cages at both sites. The North Dakota release was made in four 3.3 m^2 cages. The number of *A. flava* released ranged from 50 to 260 beetles per site, except at the 1987 Lyman Creek Sun site release, where a major collection effort resulted in 6 releases totaling 2077 beetles. This "mass" collection and release was done to learn if releasing large numbers could promote better establishment and rapid numerical increase in *A. flava* populations after establishment.

Aphthona flava established at four of the eight Montana sites and at the single North Dakota site. No recoveries have been made to date at the Idaho sites. The best Montana establishment was at the Lyman Creek Shade site, where a mark and recapture study (following unpublished techniques used by A. McClay, Vegreville, Alberta) estimated an *A. flava* population of 31/m^2 adults. A visual search and count of *A. flava* adults at the North Dakota site yielded 14/m^2 in 1988 (R. Carlson, pers. comm.) Beetles at the Reed Point and the Columbus, Montana sites were not recovered the year following release (1986), but were found in low numbers two years after release (1987). Establishment of *A. flava* was obtained with the release of only 50, 57 and 106 beetles per site. In Montana, releases made in cages resulted in establishment at three of four sites. The cage release at the North Bozeman site may have failed because of the spraying of herbicides at the site the year following release. The mass release at the Lyman Creek Sun site was the only one of four open releases in Montana that produced an establishment. Good establishment was obtained in North Dakota where cages were used but no recovery of *A. flava* has been made in Idaho where both open and cage releases were made.

There is no apparent pattern relating establishment of *A. flava* to known site characteristics or release dates.

Identification and Distinguishing Features

Aphthona flava is completely orange, has no elytral sculpturing and is large (3–4 mm) for a flea beetle. The only North America flea beetles recorded from *Euphorbia* species are *Glyptina* species. *Glyptina spuria* LeConte has been collected from *E. maculata* L., and *E. blodgettii* Engelm. ex A. Hitchc. from the east and southeastern U.S. (Wheeler 1981). *Glyptina cyanipennis* Crotch is recorded from *E. cyathophora* Murray in Florida (Schwarz 1890) and *G. atriventris* Horn adults have been found on flowers of leafy spurge in North Dakota (Julian 1984). All of these *Glyptina* species are small (≤3 mm), have regular rows of punctures on the elytra and are darkly colored (Arnett 1968). The other *Aphthona* species that have been introduced against leafy spurge are smaller (2–3 mm) and black (*A. czwalinae* Weise) or brown (*A. cyparissiae* (Koch) and *A. nigriscutis* Foudras.

Conclusion

The ability of *A. flava* to control leafy spurge has not yet been established. The beetle has not had time to increase its pop-

ulations to the point where they may begin to stress the plants. We think that the utility of *A. flava* will be as part of a complex of natural enemies, stressing different parts of the plant and in different areas of the weed's range, that may eventually control leafy spurge.

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NOTE

Two new synonyms in Rhyacophilidae (Trichoptera)

Specific identifications of Trichoptera almost invariably depend on examination of the genitalia, and principally those of the male which exhibit characteristics that are far more conspicuous than those of the female. Regarding specific characters of caddisflies McLachlan (1874, *A monographic revision and synopsis of the Trichoptera of the European fauna*. Pt. 1:1–46. London) remarked, "Colour, minor points of neuration, &c., furnish these characters in part; but the most important are found in the anal appendages, especially of the male." Over the years this method has become a well established convention in Trichopterology, and today the description of the male genitalia is essential in virtually all caddisfly species descriptions. However, in the past this method was not so universally accepted and many species that were described solely on the basis of females can only be regarded presently as *nomina dubia*. Fortunately, subsequent taxonomic contributions have made it possible to identify the females of most of the eastern North American species of *Rhyacophila*. Recent examination of the female holotypes of two species has revealed that *Rhyacophila formosa* Banks is conspecific with *vuphipes* Milne, and *mainensis* Banks with *melita* Ross. *Formosa* is a member of the *fuscula* group that includes one other species, *fuscula* (Walker). *Mainensis* is a member of the *siberica* group that includes only four other eastern species, *amicis* Ross, *atrata* Banks, *manistee* Ross, and *minor* Banks. Female descriptions of all of these species have been provided by Schmid (1981, Mém. Soc. Ent. Canada 116: 1–83), with the exception of *amicis*. However, I have examined the female of *amicis* and find that, as in the females of all the aforementioned species, it is quite distinct.

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Rhyacophila formosa Banks

Rhyacophila formosa Banks 1911, Trans. Amer. Ent. Soc. 37: 353, 355, ♀.

Rhyacophila vuphipes Milne 1936, Studies N. Amer. Trich. Cambridge, Pt. 3, pp. 99, 102, 111, fig. ♂. NEW SYNONYM.

Examination of the ♀ holotype of *formosa* [MCZC] has revealed that it matches the description of *vuphipes* provided by Schmid (1981). Thus, the latter is recognized here as a junior synonym of *formosa*. This species is widespread along the east coast of North America, but it is not especially common. Sherberger and Wallace (1971, New York Ent. Soc., 69: 43–44) mention that larvae occur in small, rocky rivers. Reliable records are known from Georgia, Massachusetts, New York, North Carolina, Ontario, Pennsylvania, Quebec, South Carolina, Tennessee, and West Virginia.

Rhyacophila mainensis Banks

Rhyacophila mainensis Banks 1911, Trans. Amer. Ent. Soc. 37: 354, ♀.

Rhyacophila melita Ross 1938, Ill. Nat. Hist. Survey Bull. 21: 104–105, f. 6, ♂. NEW SYNONYM.

Examination of the ♀ holotype of *mainensis* [MCZC] has revealed that it matches the description of *melita* provided by Schmid (1981). Therefore, the latter is recognized here as a junior synonym of *mainensis*. Reliable records are known from Maine, Massachusetts, Michigan, New Hampshire, Newfoundland, New Jersey, New York, Quebec, and West Virginia.

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PROC. ENTOMOL. SOC. WASH.
92(2), 1990, pp. 359–360

Book Review

The Plant-Feeding Gall Midges Of North America. Raymond J. Gagné. 1989. Cornell University Press, Ithaca. 356 pp. $45.00.

Gall midges, or cecidomyiids, are intriguing insects to study because they are so small and spend most of their lives wrapped in a specialized chamber provided for them by plants. Adults, the size of a comma, do not feed. They emerge to mate and lay eggs, often dying the same day. There are about 900 species of gall midges in North America. Most of them, or their galls, including the one-third which are known but not yet identified to species, are illustrated and keyed in Gagné's book.

A wide range of topics is covered in the eight chapters of this 356-page book. The chapter on biology reviews present knowledge about how gall midges select and cope with different hosts. It discusses their strategies for survival and the damage they cause to economic plants. The chapter on anatomy gives an overview of the life stages: egg, larva, pupa, and adult. A detailed discussion of third instar larval anatomy is postponed to the chapter containing the larval key. Technical terminology is kept to a minimum, and specialized words are clearly defined in the glossary. The chapter on classification reviews the history of gall midge taxonomy in North America, beginning with the Hessian fly in 1817. Problems with the naming of species are mentioned, and a summary of the gall midge genera is presented. A short chapter defines galls and their growth and diversity. It describes primary characteristics for all galls, including those made by wasps, mites, and other flies.

The book's two keys are an indication of the considerable emphasis placed on identification. Contrary to the general view, Gagné tells us morphology of the larvae and knowledge of the host are important for identification to the species level. Gagné does not give us a key to adults because adults are difficult to prepare for study and their characters are difficult to use. Both male and female are required for identification to the species. Females, by themselves, usually cannot be identified even to genus. Therefore, one chapter is a key based on the mature or third instar larvae. Another chapter, comprising over half of the book, is a key to the galls, based on the host plant and gall types, their location on the plant, and damage they cause. Couplets in both keys are well constructed and clearly worded. Knowledge of the host plant group is a necessary prerequisite for proper use of both keys but otherwise they are not difficult. The gall key may be easily used in the field for quick identifications. Another chapter discusses the collecting, rearing, and general study of gall midges. All information in the book is abundantly documented in a bibliography of over 450 references. Many of the articles cited are recent and a few are still in press, indicating thorough research and a concern for accuracy.

This hardbound book is printed on acid-free paper in an easy-to-read style. The two column format affords wide margins. There are 434 impressive half-tone drawings, all uncluttered, clear, and well labeled. Many of the drawings help to ease the user through the larval and plant keys while others illustrate important pupa and adult types. There are also four high quality, full page, colored plates showing life stages of several different gall midges and their hosts.

A few flaws in organization weaken the book somewhat. The chapters on distribution of gall midges and the morphology of the galls should have been placed before the keys rather than between them because they serve to introduce us to the subject. The chapter on collecting, rearing, and preparing gall midges for study belongs at the end. The

valuable information on evolution of gall midges is scattered throughout the book and could have been brought together to make an interesting chapter.

This is the first new book on midges in 50 years. This book, intended for the general reader, will also appeal to the professional entomologist and ecologist because it deals well with this unique group of flies and their hosts. Gagné's purpose in writing is to list all of the plant gall midges of North America and to review the current literature in order to encourage and assist the further study of these insects. He has succeeded very well in achieving these goals. This is a succinct, well conceived, and well written book.

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PROC. ENTOMOL. SOC. WASH.
92(2), 1990, p. 360

Note

A New Synonym in Hydroptilidae (Trichoptera)

In a paper about Trichoptera from Pennsylvania (Ann. Carnegie Mus. 47: 1–12, 1978) we described *Stactobiella solzhenitsyni*, unfortunately unaware of the fact that *S. martynovi* Blickle & Denning (J. Kansas Ent. Soc. 50: 287–300, 1977) was in press at the same time. We recognize here that *S. solzhenitsyni* Sykora & Weaver is a junior synonym of *S. martynovi* Blickle & Denning.

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PROC. ENTOMOL. SOC. WASH.
92(2), 1990, pp. 361–362

Book Review

Plant Stress-Insect Interactions. Edited by E. A. Heinrichs. 1988. John Wiley & Sons, New York, 492 pp. Hardcover $59.95.

E. A. Heinrichs, Entomology professor and department head at Louisiana State University, has compiled a book of thirteen chapters on plant stress and insect interactions. As the author of chapter 1, Heinrichs first reviews and categorizes plant stress, and then defines it as "any abiotic or biotic factor of the environment that affects plant physiology, chemistry, growth, and/or development in such a way that plants perform below the average for a region" (p. 10). The remaining twelve chapters review current knowledge of how plant stress (natural or man-induced) affects insects, especially pests of economically important plants, and to a lesser extent, how insects alter the impact of plant stress.

Chapters 2 through 5 describe abiotic factors of plant stress, specifically mineral nutrition, water stress, temperature-induced stress, and electromagnetic radiation. Chapters 6 through 9 review the (mostly) man-induced plant stress of insecticides, plant growth regulators, air pollution, and mechanical damage. The final four chapters address the role of insects in altering the impact of environmental stress, plant stress and natural enemy efficacy, and pathogens and weeds as stress-inducers in plant/insect interactions.

As with many edited books, the quality of the thirteen chapters varies considerably. For example, Dale's chapter on soil mineral stress and Campbell's chapter on plant growth regulators (PGR) are excellent reviews that not only discuss the complexity of the plant stress/insect interactions, but also provide a list of research needs. In contrast, some of the chapters, such as Berenbaum's on electromagnetic radiation, Altieri's on weed-induced stress, and Smith's on mechanical damage are incomplete. Although Berenbaum reviews ultraviolet radiation and plant chemistry as it affects host plant suitability, she ignores such topics as shade as a stress factor, nutritional as opposed to allelopathic effects of radiation on insects, and the direct influence of radiation on insects. Similarly, Smith's chapter on mechanical damage focuses on allelochemics as a factor in host plant suitability, but does not discuss how nutritional chemistry changes with damage.

Most of the research presented measured the response of insects to varying plant conditions, with little focus on the cause for any change in response. As Campbell states, "most reports of effects of PGRs on insect-plant interactions do not explore the chemistry of these effects and are only observations of insect performance on the treated plants" (p. 234). Entomologists need to further develop their knowledge of the mechanisms underlying these changes. In fact, Hughes's chapter on air pollution would be a good source for a graduate student research problem as he devotes about 40% of his text to methods, approaches, and research needs.

With the focus on individual topics in this book, discussion of the interrelationship of the mechanisms of plant stress falls between the chapters (although see p. 299). In addition, no general theory is developed to summarize our knowledge of plant stress/insect interactions or to provide testable predictions for future research. However, the absence of a theory may indicate that the subject is still in a descriptive stage of development. Nevertheless, to my knowledge no books preceding this one focus exclusively on plant stress/insect interactions. Instead, entomologists have had to rely on reviews found in various scientific journals. Thus, Heinrichs' book is an excellent at-

tempt to fit together some of the puzzle pieces of plant stress/insect interaction research. But other pieces are still missing, and though this will be a useful reference for insect ecology and pest management courses, it may be especially useful as a basis for future research in plant/insect interactions.

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PROC. ENTOMOL. SOC. WASH.
92(2), 1990, pp. 362–363

Book Review

Insect Spiracular Systems. By T. B. Nikam and V. V. Khole. Ellis Horwood Limited, Chichester, England and Halstead Press, New York. 1989. 136 pp.

The intent of this short book is to provide students and researchers with an introduction into the realm of spiracles and their interaction with other elements of tracheal systems. This objective was achieved, however, in a somewhat abbreviated manner and one can only wish for an expanded version.

The strong points of the text are the physiological discussions found in Chapter 3 (Environmental compulsions and relative adaptive features of spiracles), Chapter 4 (Exogenous and endogenous factors affecting the functioning of spiracles), and Chapter 7 (Insects: an air-cooled engine). Although these chapters are only 10, 14, and 11 pages, respectively, they are quite good, draw together many recent publications, and are recommended readings.

The weak parts of the text generally are found in the critical first part of the book, the comparative morphology and developmental sections. Chapter 1 on development and metamorphosis leaves the most unsaid. Although information available on embryological development of spiracles is not extensive, more should have been written because this chapter serves as the basis for the entire text. In discussing metamorphosis, the authors correctly indicate that this phenomenon imparts great alterations on the system, yet they concentrate, as exhaustively as on any other subject, on changes occurring between cyclorrhaphan larval instars (including four pages of plates where one plate would have been sufficient) and only minimal reference is made to changes appearing in the pupa and none to adult metamorphosis. Other major criticisms of this chapter include taking a sentence from Snodgrass's classic text (p. 426) that is quoted nearly verbatim on page 14 without citation; reprinting the embryo figure of *Dixippus* from Snodgrass with an obvious tracheal invagination on the first maxillary segment, yet stating that none exist in this region; leading the reader to infer that ectodermal invaginations give rise to the tracheal system at about 78 hours for all insects (page 13); referring to the integument as a skin (page 13); and stating that Holometabola undergo incomplete metamorphosis (page 17). A short discussion on the spiracular cuticle would have added important depth and aided in understanding closing mechanisms.

Chapter 2 discusses the morphology of spiracles by order and does a commendable job of presenting the comparative structure and physiology of the thoracic and first abdominal spiracles of adults. However, this

would have been an opportune place to also discuss the evolution of spiracles, to speculate on which of the four pairs of spiracles in Diplura are homologous (if any) to other insect orders, and to discuss the number of abdominal spiracles of each order (the number is cited only for adults of some orders).

Unfortunately there is no separate chapter, or major subdivision of a chapter, devoted to larval spiracles, including structure and ordinal differences and similarities. There is a wealth of data on these larval structures making this omission (except for the previously mentioned cyclorrhaphan spiracles and a few scattered references) unfortunate.

The writing style of the authors is direct and prolific in its citations; one is quickly reminded of the Annual Review volumes rather than writings in most texts. Perhaps the brevity of writing is partly the result of page limitations imposed upon the authors by publishers; if so, the work suffered from this constraint.

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PROC. ENTOMOL. SOC. WASH.
92(2), 1990, pp. 363–364

Book Review

Crop and Plant Protection: The Practical Foundation. By Rudolph Heitefuss. Ellis Horwood Limited, Chichester, England, Distributed by Halsted Press, New York. 1989, 261 pp. Cloth.

Crop protection based on the integration of all known pest management techniques is a goal of many crop production systems. To achieve this goal a thorough understanding of the principles of all aspects of crop management, along with knowledge of environmental and economic consequences due to a particular management technique, is needed. The book reviewed here attempts to provide a concise outline of current crop management practices that can be used by students and practitioners alike.

The current edition is an English translation of the original German *Pflanzenschutz,* Second Edition, published in 1987 by Georg Thieme Verlag. In general, the translation is well done with few grammatical errors. Several typographic errors were found. At times page references within the text were not complete. The use of "(see p. 000)" was noted several times. Obviously the actual page numbers of the references were not provided which caused some confusion. The book was written with 11 chapters and was illustrated adequately.

The author based much of his information on crop protection on studies conducted in western Europe, particularly the Federal Republic of Germany. Most references cited are German with some citations provided from the United Kingdom and the United States. The book is arranged in a logical manner and provides an easy to follow sequence of how crop protection programs are developed, and the means and tools with which to implement such programs. Discussions of the ecological aspects of pest management are provided as are discussions on most control measures. An interdisciplinary approach is used with fundamental ideas presented from the fields of plant pathology, nematology, entomology, weed science and crop fertility. Though the author could not provide comprehensive discussions of all included subject matter, he has done a commendable job of tying

together the needed basic information in order to make the book worthwhile to all persons interested in crop protection.

Several of the chapters included in the text provided much needed insight into the growing environmental and economic concerns faced by most agricultural producers. I was particularly intrigued with two chapters: Chapter 2, Importance of Farm Economic Management of Plant Protection; and Chapter 7, Consequences of the Use of Chemical Plant Protection Agents. These chapters provided fresh ideas on improving crop management in order to stabilize profits and improve environmental conditions associated with agriculture. The chapters provided thought provoking ideas seldom mentioned in many texts. Other chapters dealing with reduction of pest damage and the description of control tactics were well written. The chapter on direct control measures, particularly the description of chemical plant protection agents, was a bit long but does give the reader a basic background in how various pesticide family groups were derived and how they work.

In general I find this book to be a useful contribution to the science of crop protection. The integration of management techniques from all disciplines into one text is unique and provides students with an excellent reference manual. It will become a valuable edition to libraries throughout the world in spite of its emphasis on German production practices.

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92(2), 1990, pp. 365–372

Society Meetings

949th Regular Meeting—May 4, 1989

The 949th Regular Meeting of the Entomological Society of Washington was called to order by President F. Christian Thompson in the Naturalist Center, National Museum of Natural History, at 8:03 p.m. on 4 May 1989. Twenty-three members and four guests were present. Minutes of the April meeting were read and approved with one addition and one correction.

Membership Chairman G. B. White read the name of the following applicant for membership: Don Harrington, Richardson, Texas.

Gaye L. Williams exhibited a gourd decorated with arthropod motifs carved in a Mexican vein. The gourd had been sent by a former ESW member, Elaine Lowry, who now resides in the Southwest.

Edd Barrows described the Michener Retirement Conference, or "MichFest," held at the University of Kansas on 14–15 April to honor one of this century's greatest entomologists. The warmth of this occasion was amply conveyed in a series of slides that also provided glimpses of the local flora and at least one prominent Kansan declivity.

The speaker for the evening was James B. Stribling, Associate Research Professor, Department of Biology, Georgetown University, Washington, D.C. His talk, entitled "Life History of Marsh Beetles in Treeholes and Bromeliads," focused on the ecology of the Scirtidae, whose larvae are aquatic and occur in phytotelmata: plant structures that are capable of holding water, e.g. leaf bases of bromeliads, coconut shells, and depressions or hollows in trees. As a group, scirtid larvae are instantly recognizable by their long, multisegmented antennae. However, specific determinations are often impossible without rearing. Adults are terrestrial and may be collected at light traps or by beating vegetation. Dr. Stribling's extensive field experience in the United States and Central America has yielded data on larval characters and habitat specificity that together will constitute a foundation for phylogenetic studies of this family.

J. H. Fales reported that during the last two years the monarch butterfly (*Danaus plexippus* (Linnaeus)) has been virtually absent as a Spring migrant in southern Maryland. Similar observations have been made by lepidopterists in the Northeast. Fall migrations also have been poor. However, monarchs were seen moving through southern Maryland on 26 and 28 April, dates that are slightly ahead of Fales' average for first sightings, which is 1 May.

Mignon Davis thanked her two children, Marisa and Steven, for helping to make the date-nut bread and other goodies brought to this evening's meeting.

President Thompson urged the membership to turn out in force for what promises to be an especially enjoyable annual banquet.

Visitors were introduced and the meeting was adjourned at 9:18 p.m. Refreshments followed.

Richard G. Robbins, *Recording Secretary*

951st Regular Meeting—October 5, 1989

The 951st Regular Meeting of the Entomological Society of Washington was called to order by President F. Christian Thompson in the Naturalist Center, National Museum of Natural History, at 8:00 p.m. on 5 October 1989. Twenty members and five guests were present. Minutes of the May meeting were read and approved.

President Thompson praised the accomplishments of outgoing Editor Hiram G. Larew and introduced his successor, Robert D. Gordon, Systematic Entomology Laboratory, U.S. Department of Agriculture. Dr. Gordon thanked the Society for the trust it had placed in him and announced that during his tenure he would refrain from making major editorial decisions by himself. Instead, he will refer such matters to the Publications Committee, in which there have been some recent changes: Don Davis and Don Whitehead are slated to replace Bob Peterson and Rebecca Surdick. President Thompson added that there are vacancies in the roster of officers for 1990. Prospective candidates are welcome.

Recording Secretary R. G. Robbins read the names of the following applicants for membership: Richard L. Bottorff, Placerville, California; R. G. Brown, Commonwealth Agricultural Bureaux, Institute of Biocontrol, Curepe, Trinidad; Zapparoli Marzio, Instituto di Difesa Delle Piante, Viterbo, Italy; Vicente Carapia Ruiz, Departamento de Parasitologia, Universidad Autonoma Agraria "Antonio Narro," Buenavista Saitillo, Coahuila, Mexico; Chang Eon Lee, Department of Biology, College of Natural Sciences, Kyungpook National University, Taegu, South Korea; John S. Weaver III, Department of Entomology, University of New Hampshire, Durham; Charles E. Williams, Department of Biology, Washington and Lee University, Lexington, Virginia; and Michael J. Sharkey, National Institute of Agro-Environmental Sciences, Division of Entomology, Yatabe, Tsukuba, Ibaraki, Japan.

Mignon Davis circulated a sign-up sheet for volunteers to bring refreshments to our meetings.

In an evening replete with exhibits, Doug Sutherland led off by distributing copies of U.S. House of Representatives Joint Resolution 411 designating the monarch butterfly (*Danaus plexippus* (Linnaeus)) as our national insect. Introduced by Leon E. Panetta of California on 27 September of this year, the resolution reads: "Whereas the monarch butterfly, native to North America, is found throughout the United States; whereas the monarch is a unique representative of over 600 species of butterflies and nearly 90,000 other insects that are an integral part of the natural heritage of the United States; whereas the great diversity of insects play a vital role in the daily lives and ecology of the environment; whereas the population of monarchs is declining under pressure from urbanization and loss of habitat which results in the reduction of the host plant (milkweed) and overwintering groves of trees in California and Mexico; whereas conservation efforts are under way in both California and Mexico to maintain these overwintering sites; whereas Pacific Grove, California, holds an annual festival celebrating the return of the monarchs to overwinter until spring when the monarchs begin a northward flight; and whereas the monarchs enhance the beauty of the environment and signals [sic] the need for protection and conservation of the natural wonders: Now, therefore, be it resolved by the Senate and House of Representatives of the United States of America in Congress assembled, that the monarch butterfly is designated and adopted as the national insect of the United States, and the President is authorized and requested to declare such fact by proclamation." Dr. Sutherland also exhibited this October's issue of *Ranger Rick* (a young people's nature magazine published by the National Wildlife Federation), which instructs children on how to lobby for passage of H. J. Res. 411; the summer 1989 issue of *Wings* (vol. 14, no. 2, a publication of the Xerces Society), which is entirely devoted to the monarch; and this September's issue of the *Reader's Digest*, which on pages 134–136 contains an article about monarchs entitled "My Butterfly Mystery," by Jonathan Weiner.

Continuing in a lepidopterological vein, Edd Barrows displayed a larva of the tiger

swallowtail (*Papilio glaucus* Linnaeus) ("very dark this year"), a tomato hornworm (*Manduca quinquemaculata* (Haworth)) bedecked with the cocoons of a braconid parasite, a brachypterous female moth of unknown affinity, and a single live female bagworm (*Thyridopteryx ephemeraeformis* (Haworth)) together with a quarter pound of preserved suitors.

For lepidobibliophiles, Ted Spilman exhibited the new paperback *Florida Butterflies* by Eugene J. Gerberg and Ross H. Arnett, Jr., Natural Science Publications, Inc., Baltimore, Maryland, $9.95, ISBN 0-89140-031-1. Each of the true butterflies (Papilionoidea) of Florida is illustrated with a color photograph, followed by brief descriptions of one or both sexes, adult habitats, flight periods, larval food plants, and distribution in Florida. For the confusingly similar skippers (Hesperioidea), only distributions and larval hosts are listed. Ninety-seven true butterflies and 67 skippers are known to breed in Florida, which means that for both superfamilies the Sunshine State can claim over 20% of the North American fauna.

President Thompson issued a change in orders by exhibiting volume four of *Myia* (1989, Insect Associates, South San Francisco, California), a tribute to Edward Luther Kessel on the occasion of his 85th birthday. Kessel is the foremost authority on flat-footed flies (Platypezidae). Between 1947 and 1987, he and his coauthors published 56 papers in which over one third of the world's 215 known platypezid species were named and described. Dr. Thompson also displayed a souvenir of his attendance at last year's Nobel Symposium: *The Hierarchy of Life. Molecules and Morphology in Phylogenetic Analysis* (1989, Excerpta Medica, New York, ISBN 0-444-81073-0) contains the proceedings of Nobel symposium 70 held at Alfred B. Nobel's Björkborn, Karlskoga, Sweden, 29 August–2 September 1988. A descriptive brochure and photos of the symposium were circulated among the membership.

The speaker for the evening was Donald R. Whitehead, Research Entomologist, Systematic Entomology Laboratory, U.S. Department of Agriculture, whose talk was entitled "Mimetic Millipede Madness: Tropical Biology in Eastern North America." Dr. Whitehead's millipede studies have focused on the several species complexes that occur in West Virginia, where problems in geographic variation are often compounded by Müllerian mimicry and by distributions that appear to be unrelated to local drainage systems, soil types, or other environmental variables. One consequence of this chaos is that the millipede fauna of eastern North America is not yet amenable to phylogenetic analysis. However, thanks to Bob Gordon's camera caddying, we now have a good photographic record of these peripatetic arthropods.

Visitors were introduced and the meeting was adjourned at 9:20 p.m. Refreshments followed.

Richard G. Robbins, *Recording Secretary*

952nd Regular Meeting—November 2, 1989

The 952nd Regular Meeting of the Entomological Society of Washington was called to order by President F. Christian Thompson in the Naturalist Center, National Museum of Natural History, at 8:05 p.m. on 2 November 1989. Twenty members and 19 guests were present. Minutes of the October meeting were read and approved—pending determination of the correct generic name for the tomato hornworm (*vide supra*).

Membership Chairman G. B. White read the names of the following applicants for membership: John R. Linley, Medical Entomology Laboratory, Institute of Food and Agricultural Sciences, University of Florida, Vero Beach; Stuart H. McKamey, Department of Ecology and Evolutionary Bi-

ology, University of Connecticut, Storrs; and Robert W. Pemberton, Asian Parasite Laboratory, APO San Francisco, California.

Nominating Committee Chairman Ted Spilman presented the following slate of officers for 1990: President, Jeffrey R. Aldrich (automatic); President-Elect, David R. Smith; Recording Secretary, Richard G. Robbins (incumbent); Corresponding Secretary, Hollis B. Williams; Treasurer, Norman E. Woodley (incumbent); Program Chairman, Gary Steck; Membership Chairman, Geoffrey B. White (incumbent); Editor, Robert D. Gordon; Associate Editor, Thomas J. Henry; and Custodian, James B. Stribling. Ted thanked Nominating Committee members Edd Barrows and Doug Sutherland for their assistance in formulating this roster, which will be put to a vote at the December meeting.

In anticipation of this evening's presentation, Edd Barrows displayed a jar of fleas (presumably *Ctenocephalides felis* (Bouché)) from his family dog.

The speakers for the evening were Ralph P. Eckerlin, Professor, and Harry F. Painter, Professor Emeritus, Natural Sciences Division, Northern Virginia Community College, Annandale Campus, whose talk was entitled "Studies on the Fleas of Virginia." For almost two decades, these indefatigable siphonapterists have braved the elements and some quizzical citizens in an effort to catalog and comprehend the Old Dominion's little-known flea fauna. By trapping small mammals, retrieving road kills, and—perhaps most important—processing host nests in Berlese-Tullgren funnels, they have determined that flea diversity is lowest on the warm, humid coastal plain (11 species), increases in the Piedmont (17 species), and is greatest in the high mountains bordering West Virginia (26 species). Moreover, the number of flea species tends to increase from south to north, while the number of host species increases in the opposite direction. Similar observations from other parts of the world appear to confirm the general rule that flea species diversity increases as temperature and humidity decrease. Drs. Eckerlin and Painter speculate that as many as 45 flea species may be present in Virginia because much of the state lies in a transition zone between austral and boreal elements. They have recently lengthened the list of fleas from Fairfax County in northern Virginia, and they have conducted detailed investigations of the seasonal dynamics of fleas associated with the southern flying squirrel, *Glaucomys volans* (Linnaeus), in the Virginia Piedmont. Collections of fleas from any part of the state will be warmly welcomed as contributions toward an eventual monograph in the *Insects of Virginia* series, Virginia Polytechnic Institute and State University, Blacksburg.

In keeping with the evening's subject matter, R. G. Robbins could not resist the itch to introduce Dr. Robert Traub, the world's foremost authority on fleas and, by recent vote of the American Committee of Medical Entomologists, only the third recipient of the prestigious Harry Hoogstraal Commemorative Medal, which will be conferred at this year's Annual Meeting of the American Society of Tropical Medicine and Hygiene, in Honolulu, Hawaii. Though justly revered for his siphonapterological studies, Dr. Traub achieved transcendent fame for his central role in the chemoprophylaxis of chigger-borne rickettsiosis (*Rickettsia tsutsugamushi*) during and after World War II, work that earned his team a nomination for the Nobel Prize. Beyond being a renowned scientist, Dr. Traub is one of a fast-fading élite of Renaissance men that included his lifelong friend and colleague Dr. J. Ralph Audy (1914–1974), whose charming book *Red Mites and Typhus* (1968, Athlone Press, London) captured the romance of medical acarology's golden age. On this occasion, Dr. Traub was accompanied by his sprightly wife Renée; both received the warm applause of the membership.

R. G. Robbins also announced the im-

minent departure of Dr. Lance A. Durden, who has accepted a position as a Research Associate in the Department of Entomology, Auburn University. Dr. Durden's research interests center on the systematics and ecology of the sucking lice (order Anoplura). Though only 34 years old, he has already published 12 papers on Anoplura and 33 papers on other ectoparasite groups, especially fleas, ticks, and chiggers. Indeed, at the last National Conference of the Entomological Society of America (which Dr. Durden was unable to attend), Dr. K. C. Kim of Pennsylvania State University noted during an open seminar that of the world's five experts on Anoplura, Lance Durden is the only one who is under 50 years of age. In other words—and this point could not have been lost on such a perceptive audience—he has already achieved what has cost all others the better part of their careers! For the last two years, Dr. Durden has worked in Dr. Traub's laboratory at the Smithsonian's Museum Support Center in Suitland, Maryland. With a round of applause, the Recording Secretary wished Lance Godspeed and a productive tenure in Alabama.

Mignon Davis took photographs of this evening's large audience and of the five ectoparasitologists present (the latter, a group photo, did not develop). She also circulated copies of a bill (CB-74-1989) recently introduced to the Council of Prince George's County, Maryland, that, if enacted, would require developers to preserve mature trees, specimen trees, or large clumps of trees existing on subdivisible properties. Though Maryland already has proportionately less forest cover than any other mid-Atlantic state save Delaware (2,653,200 acres or just 42% of the Old Line State's area), this modest proposal is being resisted by a powerful construction lobby that caters only to Washington's ceaseless craving for Lebensraum.

Visitors were introduced and the meeting was adjourned at 9:45 p.m. Refreshments included a rainbow cake, compliments of our youngest guests, Marisa and Steven Davis.

Richard G. Robbins, *Recording Secretary*

953rd Regular Meeting—December 7, 1989

The 953rd Regular Meeting of the Entomological Society of Washington was called to order by President F. Christian Thompson in the Naturalist Center, National Museum of Natural History, at 8:00 p.m. on 7 December 1989. Twenty members and nine guests were present. Minutes of the November meeting were read and approved.

Membership Chairman G. B. White read the names of the following applicants for membership: Edward F. Connor, Department of Environmental Sciences, University of Virginia, Charlottesville; Donald F. J. Hilton, Department of Biological Sciences, Bishop's University, Lennoxville, Quebec, Canada; and David M. Pollock, Enid, Oklahoma. Chairman White also reported that the Society gained 30 new members in 1989, bringing our total to 561.

Annual reports were given by the Corresponding Secretary, Treasurer, and outgoing Editor (the last-named two read by F. C. Thompson). The President then warmly thanked all officers and volunteers for helping to maintain our Society as this nation's premier regional entomological organization.

President Thompson reviewed the slate of nominees for officers in 1990 and called for additional nominations from the floor, of which there were none. A motion was made and seconded that the slate be accepted as presented. The motion was approved by acclamation.

Mignon Davis announced that the tree preservation bill described in the Novem-

ber Minutes had been passed by the Council of Prince George's County, Maryland.

Corresponding Secretary J. M. Kingsolver exhibited three absorbing entomological texts: *Larvas de Coleoptera do Brasil,* by Cleide Costa, Sergio A. Vanin, and Sônia A. Casari-Chen, 1988, Museu de Zoologia, Universidade de São Paulo; *A Manual of Forensic Entomology,* by Kenneth G. V. Smith, 1986, British Museum (Natural History) and Comstock Publishing Associates, a division of Cornell University Press, Ithaca, New York, ISBN 0-8014-1927-1; and *Pictorial Guide to Insect Pests of Stored Food Products,* by Toshiharu Yoshida, Naoshi Watanabe, and Mochiyuki Sonda, 1989, Zenkoku Noson Kyoiku Kyokai Publishing Co., Ltd., Tokyo.

President-Elect J. R. Aldrich displayed the first offspring of a female southern green stink bug (*Nezara viridula* (Linnaeus) (Hemiptera: Pentatomidae)) collected in a field of soybeans (*Glycine max* (Linnaeus) Merrill) in Beltsville, Prince George's County, Maryland, on 4 October of this year. Apparently a victim of hurricane Hugo, this specimen was blown some 600 km north of its known range. It has subsequently provided Dr. Aldrich with six egg masses.

Edd Barrows exhibited cocoons and adults of the sawfly *Priophorus morio* (Lepeletier) (Hymenoptera: Symphyta: Tenthredinidae), together with photographs of larval damage to raspberry (*Rubus idaeus* Linnaeus). Dr. Barrows' specimens were collected in Montgomery County, Maryland, which is south of this species' range. However, the rarest of Edd's exhibits this evening were photographs of our intrepid President—afield and stalking the wily syrphid!

The speaker for the evening was Steven L. Heydon, Visiting Scientist, National Museum of Natural History, Smithsonian Institution, whose talk was entitled "Desperately Seeking *Salix*: Interactions Between a Willow Stem-galling Agromyzid and its Two Parasitoids." Galls on willow stems are frequently the work of larvae of the agromyzid fly *Hexomyza salicis* (Malloch). Adult females of this univoltine species oviposit in early May, each egg-laying event leaving a distinctive scar. First-instar larvae molt in late June, and the second instar feeds on plant fluids throughout the summer and early Fall. In late Fall, the maggots become quiescent, swelling and losing their intersegmental folds, but they regain their normal proportions just before Spring. There is no apparent third instar; if such a stage exists, it is certainly foreshortened and probably precedes pupation, which commences in Spring and lasts about three weeks. The pteromalid wasp *Sphegigaster salicinus* Heydon and LaBerge is an endoparasitoid that kills its agromyzid host as the latter is preparing to pupate; a hormonal trigger is therefore indicated. A hitherto undescribed eurytomid (*Eurytoma* n. sp.) is an ectoparasitoid in its early instars but after killing the larva of *H. salicis,* this wasp completes its development on a diet of plant materials. Since the fly larva is destroyed before it has had an opportunity to construct an exit gallery, adult eurytomids must cut through willow stems entirely on their own. Surprisingly, male willows are resistant to agromyzid galling, and even on female plants about 75% of eggs laid fail to yield galls. By the end of the first instar, mortality may approach 85%, possibly because many eggs are too deeply or shallowly situated, having been laid in the tips or bases of willow branches. Also, if two gall chambers come together, one larva invariably kills the other. Significant protection from parasitoids is afforded only to those eggs fortunate enough to have been laid under leaf petioles. Taken together, these factors may explain the sudden local extinctions so often seen in *H. salicis* populations.

W. E. Bickley reminded the membership that Honorary Member Theodore L. Bissell will be celebrating his 90th birthday on Saturday, 9 December. On behalf of your nu-

merous friends in this and other entomological societies, many more seasons of sunshine, Ted!

Among our visitors this evening were Scott E. Miller, Chairman, Department of Entomology, Bernice P. Bishop Museum, Honolulu, Hawaii, and his friend Melody Allen, Executive Director, the Xerces Society, who solicited manuscripts for that organization's journal *Wings*.

Mignon Davis thanked the several volunteers who have kindly supplied postprogram pick-me-ups this year. President Thompson then passed the gavel and the "black book" of protocol to Jeff Aldrich, who adjourned the meeting at 9:00 p.m. Cognac followed.

Richard G. Robbins, *Recording Secretary*

Reports of Officers

Treasurer's Report

SUMMARY FINANCIAL STATEMENT FOR 1989

	General Fund	Special Publications Fund	Total Assets
Assets: November 1, 1988	$21,586.59	$73,156.18	$94,742.77
Total Receipts for 1989	52,290.83	18,003.98	70,294.81
Total Disbursements for 1989	54,918.89	0.00	54,918.89
Assets: October 31, 1989	18,958.53	91,160.16	110,118.69
Net Changes in Funds	$ 2,628.06–	18,003.98	15,375.92

Norman E. Woodley, *Treasurer*

Corresponding Secretary's Summary of Major Activities for Calendar Year 1989

Letters of welcome were mailed to 32 new members. Two letters of congratulation were sent to Emeritus and Honorary members and five letters requesting information were answered. Seven letters were written thanking our guest speakers. Four letters of thanks were sent to outgoing officers and five letters were sent to those who contributed to our special fund. The membership list was published in Volume 91 of the Proceedings. Postage costs totaled $25.00.

John M. Kingsolver, *Corresponding Secretary*

Editor's Report

A total of 73 articles, 10 notes and 13 book reviews were published in 1989 for a total of 664 pages. A total of 2 genera and 43 species were newly described. Significant summary articles appeared on similarities between wing venation in dipterans and mecopterans (G. W. Byers, pp. 497–501), on the evolution of ovoviviparity in roaches (L. R. Roth, pp. 441–451) and on neem insecticides (J. D. Warthen Jr., pp. 367–388). The Society helped defray the cost of two articles per issue, on average.

Numerous reviewers helped improve the quality of manuscripts that were published. Several members of the Smithsonian staff

(USDA and Department of Entomology) were unfailingly helpful reviewers. As members of the Publications Committee, Rebecca Surdick provided extraordinary assistance in processing manuscripts, and B. V. Peterson solicited and edited the book reviews. Several Society members provided helpful suggestions regarding format and content of the Proceedings during my tenure as Editor. Carol Ann Roth, as typist, had the nearly impossible task of deciphering my handwriting. And during the last six months of 1989, Bob Gordon, as Associate Editor, came to the aid of an Editor awash in manuscripts. To all of these people, I extend my thanks. The Proceedings are truly produced as a joint effort.

Respectfully submitted,
Hiram G. Larew, *Editor*

PUBLICATIONS FOR SALE BY THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

Miscellaneous Publications

Cynipid Galls of the Eastern United States, by Lewis H. Weld	$ 5.00
Cynipid Galls of the Southwest, by Lewis H. Weld	3.00
Both papers on cynipid galls	6.00
Identification of Alaskan Black Fly Larvae, by Kathryn M. Sommerman	1.00
Unusual Scalp Dermatitis in Humans Caused by the Mite *Dermatophagoides*, by Jay R. Traver	1.00
A Short History of the Entomological Society of Washington, by Ashley B. Gurney	1.00
Pictorial Key to Species of the Genus *Anastrepha* (Diptera: Tephritidae), by George C. Steyskal	1.50
Taxonomic Studies on Fruit Flies of the Genus *Urophora* (Diptera: Tephritidae), by George C. Steyskal	2.00

Memoirs of the Entomological Society of Washington

No. 1.	The North American Bees of the Genus *Osmia*, by Grace Sandhouse. 167 pp. 1939	$15.00
No. 2.	A Classification of Larvae and Adults of the Genus *Phyllophaga*, by Adam G. Boving. 95 pp. 1942	(out of print)
No. 3.	The Nearctic Leafhoppers, a Generic Classification and Check List, by Paul Wilson Oman. 253 pp. 1949	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. 7.	Ant Larvae: Review and Synthesis, by George C. Wheeler and Jeanette Wheeler. 108 pp. 1976	11.00
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. 9.	The Flower Flies of the West Indies (Diptera: Syrphidae), by F. Christian Thompson. 200 pp. 1981	10.00
No. 10.	Recent Advances in Dipteran Systematics: Commemorative Volume in Honor of Curtis W. Sabrosky. Edited by Wayne N. Mathis and F. Christian Thompson. 227 pp. 1982	11.00
No. 11.	A Systematic Study of the Japanese Chloropidae (Diptera), by Kenkichi Kanmiya. 370 pp. 1983	18.00
No. 12.	The Holarctic Genera of Mymaridae (Hymenoptera: Chalcidoidae), by Michael E. Schauff. 67 pp. 1984	5.00
No. 13.	An Identification Manual for the North American Genera of the Family Braconidae (Hymenoptera), by Paul M. Marsh, Scott R. Shaw, and Robert A. Wharton. 98 pp. 1987	18.00

Back issues of the Proceedings of the Entomological Society of Washington are available at $25.00 per volume to non-members and $13.00 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, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560.

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PROCEEDINGS

of the

ENTOMOLOGICAL SOCIETY of WASHINGTON

PUBLISHED QUARTERLY

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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, NHB 168, Smithsonian Institution, Washington, D.C. 20560.

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 8 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 $20.00 (U.S. currency) of which $18.00 is for a subscription to the Proceedings of the Entomological Society of Washington for one year.

PROCEEDINGS.—The *Proceedings* are published quarterly beginning in January by The Entomological Society of Washington, % Department of Entomology, NHB-168, Smithsonian Institution, Washington, D.C. Members in good standing receive the Proceedings of the Entomological Society of Washington. Nonmember subscriptions are $50.00 per year, domestic, and $60.00 per year, foreign (U.S. currency), payable 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 P. 318 OF THE APRIL, 1989 ISSUE FOR INFORMATION REGARDING PREPARATION OF MANUSCRIPTS.

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LIKELY CAUSES AND EXPLANATION OF PROBABLE ATAVISM IN A SOMATICALLY MOSAIC FLY FROM A WILD POPULATION (DIPTERA, ASILIDAE, *NANNOCYRTOPOGON MINUTUS*)

KENNETH W. COOPER

Department of Biology, University of California, Riverside.

Abstract.—Description is given of an otherwise normal male asilid (of a genus of 28 species having either hyaline or lightly infuscated wings) with its left wing strikingly color-patterned. This appears to be the first recorded not-gynandromorphic, not-parasitized somatic mosaic in Diptera apart from laboratory cultures and experiments. Possible genetic origins of such mosaicism, of phenotypic expression, and their consequences are outlined. Despite lack of relevant fossils, the more plausible conclusion is that the wing pattern is primarily atavistic and not a neomorphism. Mutants calling forth ancestral attributes do not differ qualitatively from those altering familiar, "lesser" phenotypes. Ancestral phenotypic attributes probably regularly disappear long before their genetic mechanisms pass beyond the capacity for reexpression, as substantiated by disappearance and reoccurrence of R_3 in Brachycera.

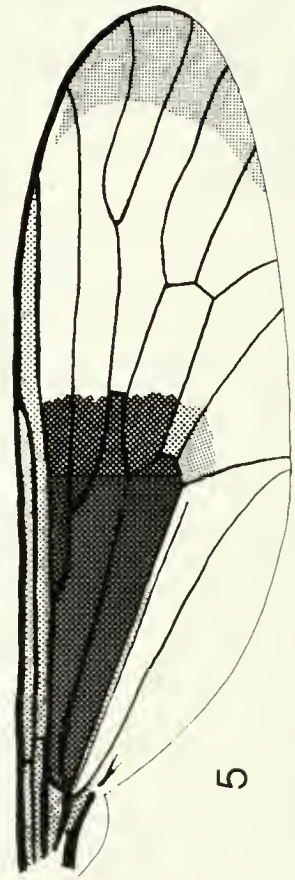
Key Words: Atavism, somatic mosaicism, genetics, wing maculation, wing venation

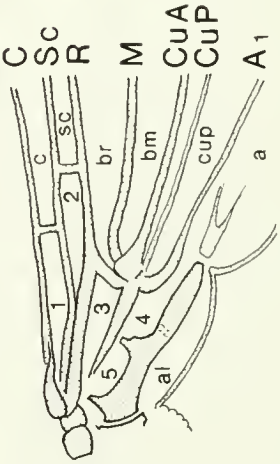
What is to be made of a chimaeric male robber fly, *Nannocyrtopogon minutus* Wilcox and Martin, otherwise normal, having the blade of one wing palely infuscate and normal for the species, the other wing displaying a striking color pattern that is unusual even among asilid species normally having maculated wings (Figs. 1–3, 5)? This in a genus in which the 28 other species do not have color patterns on their wings, being nearly equally divided between those with hyaline and those with lightly tinted wing membranes. The explanation must largely be genetic.

Because genetic systems are subject to mutation, errors of mitosis and fertilization, individuals of a population may be viewed as having their bodies potentially subjected to partition into two or more genetically different sectors during development. In most species, individuals are regarded as "normal" if no disparate sector is detected. Those having from more than 0 to as much as 50% included in such sectors are termed *mosaics*.

Though ordinarily rare, the commonest mosaic detected in wild populations of insects is the gynandromorph, in which the body is partitioned into genetically and phenotypically sexual sectors. Such sexual mosaics, not to be confused with intersexes which are of uniform genotype, have been found in many orders of insects and in many families of flies, though not in the Asilidae.[1]

[1] No museum dipterist of whom I inquired could recollect having read of or seen any mosaic *asilid* (either gynandromorphic or not-gynandromorphic). It is unlikely that striking anomalies of asilids go unnoticed (e.g. see Weinberg 1973). Yet no asilid gynandromorph or other mosaic is recorded by either Zoological Record or Entomological Abstracts (to Volume 20(5), June 1989) within the years they cover for the interval 1925–1989, nor did Collin (1927) mention any earlier records in his brief review.





1 2 3 4 5

Mosaics of a single sex, with an aspect sufficiently striking to be noticed, are well-known but not common in Lepidoptera (Cockayne 1924, Robinson 1971) where striking individual variations in color patterns of wings rarely escape notice. Elsewhere among insects, as with flies in wild populations, they appear to be of a second order of rarity. Apart from certain Nematocera infested with parasites, those recorded for Diptera, of which I am aware, are derived from laboratory cultures and experiments. The earliest general account is that by Morgan and Bridges (1919) for *Drosophila.*

It is assumed that the genetics of asilids, like that of most functionally diploid insects which have been studied, does not depart in any general or unique way from that of species of *Drosophila.* The phenotypic effects of asterisked mutant alleles of *D. melanogaster* Meigen mentioned in discussion (e.g. *Lyra), unless another reference is given, will be found in Lindsley and Grell (1963).

There are accordingly two probable answers to the large question posed by the mosaic asilid, each with more than one possible explanation. They are: the left wing of the mosaic fly may provide a preview of a remarkable apomorphy potentially realizable in the future, or it may display in near entirety a purely atavistic trait.

The Capture

The male mosaic was one of a total of 5 males and 2 females of *N. minutus* collected on July 20 and 26, 1988; the second search was made with the hope that others would be found, perhaps with both wings maculated. The site is approximately 5.2 km northwest of Fawnskin, San Bernardino Co., Ca., at an altitude of roughly 1890 m, not far from some of the formerly recorded sites at which *N. minutus* has been collected. The species is probably generally distributed in the San Gabriel and San Bernardino Mountains (Wilcox and Martin 1957).

At mid-day *N. minutus* sallied after smaller flies from perches on boulders, 30–50 cm in diameter, in the dry bed of Holcomb Creek. Most flies were old, to judge from the torn hind margins of the wings and broken or missing macrochaetae. Oddly, they were found only along a particular length of the creek bed, some 30–40 m long. The total number of individuals along that stretch was almost certainly fewer than two dozen, but more than twelve.

Normal Wing Coloration and Structure

Because the left wing of the mosaic is strikingly unusual by having a color pattern, it was necessary to determine whether it also differs in less obvious features. Though Wilcox and Martin's (1936b) description of *N. minutus* portrays the overall appearance of the fly, the account of the wing is not adequate for close comparison. The following condensed description is drawn from wings of the six normal individuals collected at Holcomb Creek, ten from the University of California collection at Riverside, and from

←

Figs. 1–5. Figs. 1–3. Mosaic male of *Nannocyrtopogon minutus* Wilcox and Martin, ca. 13× magnification (actual wing length 4.2 mm). 1—Left side, 2—dorsal aspect, 3—tilted to display right wing. Fig. 4. Diagram of flattened wing base—the proximal portion of radius has folded over the basal half of the basisubcostal cell, 2. Veins: C—costa, Sc—subcosta, R—radius, M—media, CuA—anterior cubitus, CuP—posterior cubitus, A—first anal vein. Lettered cells: c—costal, sc—subcostal, br—basiradial, bm—basimedial, cup—posterior cubital, a—anal. Numbered cells and cell-like enclosures at wing base: 1—basicostal, 2—basisubcostal, 3—first basimedial, stem or prearculus cell, 4—basianal cell, anterior to distal limb of 3rd axillary sclerite, 5—"cell" anterior to proximal limb of 3rd axillary sclerite (the only hyaline cell at the base of the wing). Other: al—alula. Fig. 5. Diagram of patterned areas and venation of left wing of mosaic male (cf. Fig. 1) roughly portraying depths of coloring and extent of pattern—see description for details of pattern.

the right wing of the chimaera. Vein color was viewed by reflected light, wing membrane color by transmitted light. The smallest details mentioned, and common to all, were determined at a magnification of 50×, and checked at 250× in two wings softened with KOH and mounted in euparal.[2] Where possible, nomenclature of veins and cells (Fig. 4) follows McAlpine (1981).

As usual, fluting of wing along longitudinal veins pronounced; veins dark sepia, somewhat lighter as they thin distally; vein MA (arculus), crossvein sc-r, veins CuP and A_2 weakly developed; membrane hyaline throughout, coloring microtrichial (properly acanthal, type b [Richards 1979]); cell c subhyaline to very pale fuscous; cells bc, bsc, stem cell [Shannon's (1924) "prearculus cell"], extreme base of cell a_1, pale to light brown; "cell" bounded above by proximal stem of MP to A_1-complex, and anterior basal portion and proximal lateral apophysis of third axillary sclerite, hyaline (Fig. 4, "cell" 5); cell sc light brown in apical half; short, pale brown streak proximally between veins CuA and CuP in some; a broad, bare hyaline band along length of posterior margin of CuP; remaining membranous areas of wing very light to pale brown, gradually paler posteriorly and basally; alula in part very pale brown, or not (Fig. 4, a1).

The Mosaic

Apart from the surprising 3-partite coloration of 3 grades of saturation marking the blade of the left wing (Figs. 1, 2, 5), a slightly more exaggerated fluting along its longitudinal veins, and minor defects to be discussed, the mosaic specimen is a normal male. In appearance it corresponds well with Wilcox and Martin's description. External morphology of head, antennae,[3] thorax, abdomen, terminalia, legs, patterns of pruinosity and setation, right wing coloration, sizes and venational patterns of both wings (cf. Figs. 1, 3), and body coloring—even at the regions of the thorax bearing the wings—are typical of *N. minutus*.

Left wing stalk, venation, color of the five small "cells" at the stalk of the wing, and general light to pale acanthal browning of all unaffected areas of the wing blade normal for the species. Both membrane and acanthae are colored brown in sharply delimited regions of the blade, giving a much darker, large basal area and a smaller, much less dark one apically, separated by a continuous broad region of a normal light to pale tint (Figs. 1, 2, 5). Thus: cell c pale brown, lighter distally; cell sc light brown from origin to apex, cell br dark brown, somewhat lighter along anterior half; cell bm dark brown, narrowly paler in proximal third along vein CuA; bases of cells r_1 and r_{2+3} dark brown nearly to a line connecting the distal end of vein Sc to crossvein r-m; r_1 lighter along veins R_1 and R_{4+5}; nearly basal 0.4 of cell d (to a point below cross vein r-m) dark brown, darkest basally and along veins M_{1+2} and M_3; basal 0.3+ of cell m_3 and basal third of CuA successively lighter brown. Except at apex, remainder of blade very light to pale brown as in the unaffected right wing. Basal half of wing therefore presents a strongly contrasting dark brown macula in the shape of a slightly opened fan, given added emphasis by the fluting of the wing along the longitudinal veins.

Wing tip with a sharply bounded apical lunule, extending from near apex of cell r_1 to near midpoint of outer margin of cell m_2; greatest width at cell R_4 nearly one-eighth length of wing; much paler than most of

[2] At 250×, slide preparations show an approximately 12-partite internal "annulation" of MP, or bulla, immediately before its bifurcation, without a thyridial clear spot, that is not ordinarily detectable at 50× in pinned specimens. Campaniform sensilla occur along the basal margin of the tegula (*ca.* 18), at base of Sc (20±) and adjacent to its junction with crossvein h (8–9), at base of vein R (*ca.* 70) and widely scattered along its length (6–8) just before and following separation of Rs.

[3] Broken off during photography.

basal "fan," similar in lightness to coloration at base of cell cua only; everywhere contrasting strongly with the lightly tinted adjacent membrane (Figs. 1, 2, 5); alula palely infuscate.

Developmental Defects of the Maculated Wing

The left wing's length (corrected for curvature), veins, venational pattern of cells, and outlines of the wing's margin are all normal. Apart from a slight positive curvature of the blade, physical abnormalities occur in pigmented areas only and appear minor; indeed, detectable only at higher magnifications. At 25×, seven tiny dorsal blisters are visible: two near the distal end of cell bm (70 and 40 μm in greatest diameters), and five in the lunule: one in cell r_3 (20 μm); one in r_4 (30 μm); and three in m_1 (10–20 μm). At 50×, the dorsal membranes over the maculae seem very slightly thicker than the surrounding not-maculated membrane.

These abnormalities are explicable as results of a slight but consistent incoordination during the terminal stages of dorsoventral epithelial contraction of the pupal wing. Their minor nature contrasts markedly with the often extreme abnormalities to be seen among the phenotypes of mutant genes affecting the wings of *Drosophila* (see Waddington 1940, 1942).

Asilid Wing Patterns

Most asilid wings derive their coloration, when present, from type B acanthae, from membrane pigmentation, or from both; rarely is it structural. The wings of the majority of Nearctic asilids range from hyaline through tinged to full color (usually browns to nearly black), or have a gradually deepening color along an axis. A minority have discrete, maculated patterns. The commonest of these is a slight clouding or spotting at crossveins and venational branchpoints. Somewhat less frequent, but widespread, is a darkening of the wing adjacent to the apex, often in the form of a lunule.

Nearly the full range of wing coloration is shown by Nearctic species of *Cyrtopogon,* of which there are some seventy, and from which *Nannocyrtopogon* was split by Wilcox and Martin (1936a). Some, as *C. dasyllis* Williston, *C. maculipennis* (Macquart), and the male of *C. bimacula* (Walker), have large, striking patterns, but in each the principal macula is not proximal, nor is the apex maculate. As Dr. Eric Fisher pointed out to me, however, at least three Palearctic species of *Crytopogon* do have a truly apical macula separated by clear membrane from a more basal pattern; e.g. *C. centralis* Loew, the most similar of these (see Engle 1929, fig. 222, p. 355). Nevertheless, the basal macula of *C. centralis* (apically very similar in outline and extent to that of the mosaic) does not reach the base of the wing, nor is the apical macula a lunule. Though wing patterns of some *Cyrtopogon* seem not far removed, none is wholly like that of the left wing of *N. minutus.* Indeed, none of the species of the other forty-six genera of Nearctic Dasypogoninae[4] have a compound basal and apical pattern closely similar to that of the chimaera, nor do the remaining Nearctic asilids. How then is the occurrence of the two differently colored wings of the aberrant male fly to be explained, and how may the uniqueness of the patterned wing be understood?

Interpretation

Because the patterned wing of the male chimaera is free of striking abnormality in form, basal coloring, veins, and venational pattern, it is unlikely to have been the direct result of an asymmetrically directed envi-

[4] The Dasypogoninae of Martin's and Wilcox' (1965) classification have been split into three allied subfamilies by both Papavero (1973) and Lehr (1988); in North America we have: Dasypogoninae (11 genera), Stenopogoninae (31 genera), and Trigonomiminae (= Trigomiminae of Lehr; 4 genera). *Nannocyrtopogon* and its allies are stenopogonines.

ronmental influence. Even were it so, to have responded to that external stimulus in the manner required, the fly's genotype necessarily included within its repertoire an otherwise unexpressed capacity to provide the biochemical and developmental prerequisites for production of a nearly unblemished wing with that particular pattern, as later explained. If an external influence was involved, most probably it only indirectly instigated the necessary genotypic response (see below).

Among many conceivable genetic explanations, two well-known sporadic events may equally well account for the patterned wing. Because male asilids of known karyotype are either XY or XO, and females XX (Makino 1951, Cooper, unpublished), the fact that the chimaera is a male places a different restraint on the nature of the chromosome involved in each case. These events are:

1) Somatic mutation of a gene in the differential segment of a *sex chromosome* (+s/o → s/o),[5] the new allele's recessive phenotype therefore being expressible in its present hemizygous state. The mutation may have arisen by action of an external agent (e.g. by environmental radiation, mutagens, etc.), or internally (by replicative error, transposon, etc.).
2) Somatic crossing-over (see Stern 1968) in an *autosomal* heterozygote for an allele (a) giving a recessive phenotype, namely (+a/a → a/a and +a/+a equally). Studies of such crossing-over in *Drosophila* led Stern (1936) to conclude that it may in fact prove the most likely cause of somatic mosaicism *when* suitable heterozygosity is present.

If the frequency of the allele (a) were as high (but no higher) than 0.17 in the population of *N. minutus*, more than 160 flies (a number considerably larger than that of the reported and probable specimens now in collections) would be required for a 99% likelihood that at least one (a/a) individual with both wings patterned would be included within the sample. None has been reported, or described as a new species, as would be likely had such a specimen been found. The requisite heterozygotes (+a/a), however, would be relatively common (*ca.* 28% of both sexes).

In both cases the genetic change is assumed to involve an allele giving a recessive phenotype because most realized mutants with dominant phenotypes are far less common and more likely to produce malformations (catalog in Lindsley and Grell 1968). The change would necessarily occur in a nucleus at an early cleavage division of a preblastodermic egg. In that way a cell of a new genotype (either s/o or a/a) could have given rise to a sufficiently large clone to have formed the imaginal disc of the left wing, and perhaps other tissues of the chimaera. A mosaic arising from somatic crossing-over after the first "cleavage" division would be a trisectorial mosaic, in contrast to the bisectorial mosaic produced by a single somatic mutation.

Discussion

However the mosaic arose, it is clear that identical modes of genic action may be ascribed to the mutant allele, whether new (s) or preexistent (a). Choices for the results of such genic action in the case of the mosaic are two: (1) a discontinuous phenotypic change qualitatively different from that of wild type, a complex phenotype without precedent; in effect a preview of a potential apomorphy in the descendants of *N. minutus*; or (2) a recovery of an ancestral wing pattern, or nearly so; an atavistic expression which, were it found characteristic of a population today, would no doubt be viewed as an apomorphy.

Whether newly mutated or not, a struc-

[5] The "o" in these formulae indicates that there is no genic portion of the alternative sex chromosome, if any, that possesses the wild-type allele (+s), or a gene that suppresses the phenotypic action of (s).

tural gene does but one thing: it codes for the production of a single product. For many mutants, perhaps most, that product ultimately may play an active role in more than one biochemical pathway in development, giving rise to one or more seemingly unrelated phenotypic effects. Such an allele is said to be "pleiotropic" in its action. Thus *Lyra of *D. melanogaster* affects the eyes, body setae, wings, abdominal tergites and color; when homozygous it is lethal.

Of the thousand or more loci for which mutant alleles are now known in *D. melanogaster* (Lindsley and Grell 1968—"... reasonably complete through 1966"), most of the alleles have adverse pleiotropic effects. Alleles at nearly a third of the loci have an effect upon the wings, and about an eighth affect only the wings in one or more ways (catalog in Braver 1956). The phenotypic changes in the wings are almost always anomalous, among which are minor to extreme abnormalities of the blade, of its margins, of venation, of acanthae, of color, retention of hemolymph, and of expansion of the pupal wing at eclosion. Though many *Drosophila* species have maculated wings, including males of some members of the *melanogaster* subgenus (*Sophophora*) Bock and Wheeler (1972), none of the known phenotypes of male or female *D. melanogaster* take the form of a wing with a color *pattern.*

Those mutant alleles which do produce a new coloration of the blade without accompanying abnormalities of the wing are but a tiny minority of all; e.g. fuliginosus (Buzzati-Traverso 1947), *lemon, *pallid and *yellow. All such alleles at the four loci, except one (y^{50b25}, Gianotti 1951), affect both body and wing color in similar ways. Their primary effect is evidently upon the capacity of epidermal cells to produce particular melanins rather than an exclusive effect upon the epidermal cells of the wing itself. The latter appears to have been the case for y^{50b25}.

If the very extensive observations on *Drosophila* reflect in a general way attributes of mutations of flies, then comparable mutational changes affecting only coloration of the blade of the wing are expected to be extremely uncommon.

Compared with the mutant alleles that affect the wings of *D. melanogaster,* that presumed in *N. minutus* to have brought about maculation of the left wing is astonishing in the complexity of its phenotype and freedom from gross malformation. The phenotype leaves coloration of the small venational "cells" in the stalk of the wing (Fig. 4, "cells" 1–5) and most of the membrane of the blade unaffected (Figs. 1–3). However, it selectively heightens the levels of pigmentation, to very different degrees, in two unequally shaped, large, well-separated groups of contiguous epidermal cells (cf. Figs. 3 and 1, 2, 5). The pigmentation of the newly maculated areas is cell-produced and cell-limited; the boundaries between pigment cells and adjoining normally colored membrane are therefore sharply defined. Even venational cells r_1 and r_{2+3}, the bases and apices of which are of greatly different intensities of brown, show not the slightest signs of a decreasing color gradient from dark to light.

If all this resulted from a single product coded by a new allele, that product must have enhanced pigment formation (which awakens no problem) yet have benignly activated a series of coordinated pathways not ordinarily revealed by a difference in pigmentation basally and apically, nor by any partitioning of the wing into such special domains other than by veins. No mutations recorded for *D. melanogaster* produce *de novo* comparably complex, well-ordered phenotypes in any structure without notable abnormality. The circumstances appear to call for another interpretation of the origin of the pattern.

In perhaps most populations there is a phenotypically unexpressed retention of genetic bases for one or more ancestral attributes. Indeed Garcia-Bellido (1983) commented that "... it is not impossible ...

that most new patterns found in evolved groups of *Drosophila* are ancestral patterns."[6] In fact, Richards (1958) has demonstrated just such a case in *Ephestia*. Furthermore, Sondhi (1962), by continued selection in a strain of *D. melanogaster*, was able to produce a wholly new pair of bristles, in a particular location, comparable and presumably homologous with those found in the related family Aulacigastridae, and very probably with those in an ancestor of the two families. Causes and means for continuance of such apparently "silent" genic presences within the genome are discussed by Regal (1977), Riedl (1977), Hall (1984), and Coyne and Prout (1984) among others, along with examples from a variety of reactivated phenotypic expressions of such concealed bases of ancestral attributes otherwise known only from fossils. Gauld and Mound (1982) have discussed apparently frequent reversals and the problems they necessarily awaken in phyletic analysis.

To most there would seem to be an unbridgeable gap of complexity between most "ordinary" mutations and one that seems to call forth a probable attribute of an ancestor of countless generations removed. Is that so?

A mutant allele that restores the expression of an ancestral attribute does not differ from other mutant alleles with less striking phenotpes in kind, in degree, in mode of action in a developmental pathway, or even necessarily in the phyletic age of the pathway affected. It differs solely by its chance triggering and disclosure of a latent, ancient, yet still potentially expressible system within the genome. The difference is therefore not the nature of the mutation, but resides in a special peculiarity of the genome itself—a retained but suppressed integrated system, a "prepattern," in this case for wing maculation.

[6] I would add "perhaps most often in a somewhat modified form because of their reexpression within a changed genetic milieu."

The mutant allele codes for a product just as in other cases, but that product makes biochemically possible release and expression, wholly or in part, of the existant coordinated but "silent" ancestral pathways within the present genetic system. No chance pleiotropic concatenation of pathways to produce a coordinated wing pattern need be involved—that Achilles heel of the hypothesis of a wholly new phenotype. They already exist in a coordinate relation owing to prior evolution. The minor abnormalities expressed in the patterned wing of the mosaic may owe either to a pleiotropic effect of the mutant, or they may reflect a loosening of developmental timing within the retained ancestral system now being reexpressed against the milieu of new mutations accumulated since suppression of the ancestral wing pattern became a lineage attribute, or both. In any case, the reappearance of an ancestral wing pattern (or close thereto, perfect reversion being unlikely) seems to me the more plausible interpretation of the left wing of the mosaic *N. minutus*.

In the absence of evidence from fossils[7] of likely ancestral stocks, atavism cannot be disproven or proven for the wing of the mosaic. Nevertheless it does seem plausible because the complex maculated pattern in a nearly perfect wing of *N. minutus* appears otherwise as a freak of nature, for all 28 species of *Nannocyrtopogon* have either hyaline or lightly infuscated wings. However, as earlier mentioned certain species of

[7] The relevant Oligocene-Miocene fossils are assigned by their authors to stenopogonine genera contemporaneous with *Cyrtopogon* and *Nannocyrtopogon* (namely *Ceraturgus* [as *Ceraturgopsis*], 1 sp.; *Dioctria*, 2 spp.; *Holopogon*, 2 spp.; and *Microstylum*, 1 or 2 spp.). See Hull (1962) and Papavero (1973) for references and comment. So far as can be told all have either hyaline, not-maculated, or infumated wings. However, absence of maculations in a fossilized wing is not of itself reliable evidence for a corresponding absence of color pattern in the wing prior to fossilization (see Carpenter 1971).

the presumed sister group, *Cyrtopogon*, do have strongly maculated wings of interrelated patterns, some with both a central and apical macula. Those patterns are somewhat less complex, and the maculations differently shaped, defined, and placed than those of the left wing of the mosaic. Because *de novo* origin of such a complex pattern by a single mutation is highly improbable, and by simultaneous multiple mutations implausible, it is reasonble to assume that *Cyrtopogon* and *Nannocyrtopogon* shared an ancestor with a patterned wing, and that the means for wing patterning was retained in both lineages.[8] In the line from which *Nannocyrtopogon* species were derived, however, expression of pattern was suppressed. Retention of the suite of ancestral mutants involved presumably owes to their still essential contribution to one or more stages of development. Only their inessential actions, as those leading to an expression of a pattern, are genetically suppressed. The new mutant (s) or homozygote (a/a) then codes for a product of which the ultimate effect is reactivation of suppressed pattern pathways.

I now turn to another atavism, widespread among asilids and other Brachycera, that does not appear to have received the attention merited. Hennig (1954) raised the question as to whether the presence of vein R_3 in the asilid *Promachus* and its apocleine relatives represents an atavism. He thought not, although he left the question open for mydids and possibly others in which only the distal stub of R_3 or its trace remains. R_3 occurs also in the genus *Pseudorus* which is only remotely related to *Promachus* (Papavero 1973). Shannon and Bromley (1924) indicated the presence of R_3 in *Pogonosoma*, another asilid of rather remote affinity to both *Pseudorus* and *Promachus*, and in one or another form in other asilids, many bombyliids, some leptids, mydids, tabanids and occasionally in therevids. Very likely R_3 in these and perhaps other families is a vein tending to widespread reduction and loss at individually different rates throughout the Brachycera (in many families it has already been lost), a kind of "orthogenesis," much as appears to be happening to the basal length of M in flight wings of beetles.

The isolated, regular occurrence of a *complete* R_3 in certain species of *Pseudorus* (as Papavero 1973 suggests; see figs. 4, 5 in Oldroyd 1964), and in the 18 or so species of *Pogonosoma*, may represent recurrences rather than prolonged retention of R_3 beyond that of the numerous other members of their subfamilies. Certainly the well-known "anomalous" occurrences, most frequently asymmetrically, of a remnant of R_3 (as a "stump vein," = Tillyard's 1919 "interradial crossvein") or, more rarely, in complete form in individuals of species normally lacking all traces of R_3, are to be regarded as atavisms. Such individuals demonstrate that suppression of the R_3 phenotype is still not complete in their species, and that frequency and penetrance are low for the gene(s) still capable of restoring the phenotype. Unlike the maculated wing of the mosaic *N. minutus*, such cases do not require genetic mosaicism.

The general notion that the loss of an attribute in evolution, especially loss of a complex one, tends to be unrecoverable in later descendants was first proposed by Meyrick (1884), and apparently independently by Schlosser (1890), Gadow (1893), Dollo (1893) and, for plants, by Arber (1919). Such "lost" attributes, perhaps most of them, probably become unrecoverable in recognizable form only long after complete disappearance by genetic inactivation of their obvious phenotypic expression from a population. That is, only after potential co-

[8] Contrary to Meijere's (1907) opinion, ancestral flies, especially those of the Nematocera and of early Asilomorpha, probably did not have hyaline wings (all had epidermal "melanin"-producing pathways). Probably wing maculations of one sort or another were at least as common among them as they are among modern forms.

ordination of their genetic bases has finally been lost from the genome are they beyond mutational recall.

Loss of a phenotypic attribute and total loss of its recoverability have different immediate causes, and probably regularly occur stepwise over long but varying intervals of time. Just as that last known occurrence of an extinct form gives an unreliable date for *de facto* extinction (witness the coelacanth *Latimeria*), so also the time of final loss of recoverability of an apparently vanished attribute within a lineage must generally remain a matter of guesswork.

Conclusion

Though both somatic crossing-over and somatic mutation (or still less frequent genetic events) may formally account for the origin of the mosaic's patterned wing by reactivation of suppressed genetic pathways of distant ancestors, somatic mutation seems the simpler, more likely hypothesis. Both hypotheses predict certain possible outcomes by which they may be differentiated:

If the mosaicism was caused by somatic crossing-over in a fly of a population carrying an autosomal allele established at a moderate frequency, whether or not spermatogonial cells were included within the new (a/a) section, it is possible that a male or female will be found with both wings displaying the striking new color pattern in one or another population of *N. minutus*. No significant sexual difference in frequency would be expected were numbers of such flies found. Additionally, similar wing mosaics may turn up in the future because conditions for their formation are present in the population.

On the other hand, if a newly mutated sex-linked gene (s) were the cause of the mosaicism, no future finding of individuals with both wings maculated would be expected unless the mutant sector included at least some spermatogonial cells in addition to the left wing's imaginal disc. Even so there would be but a small likelihood of (s) entering and persisting in the local population at Holcomb Valley. It would depend on the male's success in leaving (s/+) female progeny, sampling error, and local population size. If (s) did persist in the population, no flies with maculated wings would be expected in the first filial generation. Thereafter males with maculated wings, though rare, would be greatly more frequent (about two orders of magnitude) than such females. If (s) did not persist in the population, reoccurrence of a similar wing mosaic, or of flies with patterned wings, would require a new mutation to the same allele or an isoallele.

Deposition of Specimen

For the present the specimen remains in my possession.

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A MORPHOLOGICAL, ALLOZYMIC, AND KARYOTYPIC ASSESSMENT OF THE PHYLOGENY OF SOME LOWER TERMITES (ISOPTERA: KALOTERMITIDAE)

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Abstract.—Ten species of termites in the family Kalotermitidae were examined morphologically, electrophoretically, and chromosomally. The assignment of the recently described species *Neotermes luykxi* Nickle and Collins 1989, to the genus *Neotermes*, originally made solely on morphological grounds, is supported by the electrophoretic data. *Neotermes castaneus*, however, appears to be a sister group to other species of *Neotermes* and *Incisitermes*. Observations on the chromosomes suggest that centric fusions, translocations involving the sex chromosomes, and discrete genome amplification events have all been involved in karyotype evolution in these termites, but a phylogeny based on chromosomal changes alone does not agree with the morphological and electrophoretic data. The observations suggest that chromosomal changes may be too rapid and widespread to be of use in constructing phylogenies in these insects.

Key Words: termites, *Neotermes*, enzymes, chromosomes, cladistics

This morphological, allozymic, and chromosomal survey of several kalotermitid termites from Florida (and a few from elsewhere) was undertaken for two reasons: first, to clarify the systematic position of the newly described species *Neotermes luykxi* (Nickle and Collins 1989); and second, to try to resolve an apparent conflict between the karyotypic relations of some members of the family Kalotermitidae (Luykx and Syren 1979) and the systematic relations as described by Krishna (1961).

Preliminary observations on *Neotermes luykxi* had at first suggested that it might simply be a morphological variant of *Neotermes jouteli* (Banks), but chromosome counts and preliminary electrophoretic data suggested a closer relation to another Florida termite, *Incisitermes snyderi* (Light). A comparison of the new species with a wider range of other kalotermitids was therefore required. In this paper we report the results of an allozymic, morphological and karyotypic comparison of the new species with nine other kalotermitid species.

Early chromosome studies on kalotermitid termites from south Florida (Syren and Luykx 1977, Luykx and Syren 1979) revealed the presence of sex-linked translocations in several species belonging to different genera, but other species in the same genera lacked them. Neither in the presence or absence of these translocations, nor in the chromosome numbers, did there seem to be much correlation between karyotype and systematic position. Therefore this study was undertaken to re-evaluate, using modern cladistic methods, the phylogeny of the

Table 1. Species of termites used in the electrophoretic studies.

Genus, Species	Colony i.d. No.	Collecting Sites	Number of Genomes Sampled
Cryptotermes			
cavifrons Banks	547	Elliott Key, FL	4
Incisitermes			
milleri (Emerson)	357	Mona Island, PR	4
minor (Hagen)	5C	Lafayette, CA	4
schwarzi (Banks)	490, 540	N. Miami, FL	8
snyderi (Light)	541	Hollywood, FL	4
Neotermes			
castaneus (Burmeister)	551	Miami, FL	4
jouteli (Banks)	*	Southern Florida	14
luykxi Nickle & Collins	466, 543	Hollywood, FL	7
mona (Banks)	361A	Mona Island, PR	4
Pterotermes			
occidentis (Walker)	91-N2-125	Tucson, AZ	4

* Colonies 432 (Knight Key), 454 (Bokeelia), 463 (Fakahatchee Strand), 465 (Dania), and 527 (Hollywood).

termites whose karyotypes had already been described in a preliminary way. The karyotypes are described in more detail, and the results are evaluated with regard to the question of the role of chromosome changes in speciation in these insects.

Materials and Methods

Termite colonies were maintained in the laboratory on the wood in which they were collected, for periods of time ranging from one month to two years. For the electrophoretic studies, individual termites were homogenized in one or two drops of dilute buffer (0.03 M Tris-citrate, pH 8.5), and the homogenates were absorbed onto filter paper wicks. Electrophoresis was carried out on 12% horizontal starch gels, using a 1:1 mixture of starch from Electrostarch Co. (Madison, Wisconsin) and Connaught Laboratories Ltd. (Willowdale, Ontario, Canada), with either the Tris-citrate buffer system (pH 8.5) described by Ridgway et al. (1970), or 0.01 M Tris-citrate at pH 6.7. Gel slices were stained according to standard procedures described by Yang (1971) and Harris and Hopkinson (1976). In all cases where there was any doubt about the relative migration rates of electromorphs from different species, the samples from the questionable species were re-run side-by-side.

An average of 5 worker termites from each colony were used. Since each colony is a single family (the king, the queen, and their offspring; Santos and Luykx 1985), a single worker from a colony represents two parental genomes, a sample of two workers represents (on average) three parental genomes, and in a sample of 5 workers the probability is .93 that all four parental genomes are represented. The number of genomes sampled for each species, along with the locations of collecting sites, is given in Table 1.

Chromosome preparations of meiotic and mitotic cells were made from the testes of reproductive males by methods described earlier (Luykx and Syren 1979, Luykx 1983). Meiotic cells provided the best material for determining the presence or absence of translocations involving sex chromosomes, while mitotic cells were best for determining the number of acrocentric and metacentric chromosomes. For a few species, only a small amount of material was available, and occasionally the quality of the chromosome

preparations from these species left some uncertainty as to the exact number of metacentrics present in the karyotype. The numbers given represent our best estimates of metacentrics vs. acrocentrics; we consider it unlikely that they are in error by more than ±1 (haploid), a margin of error that does not affect our general conclusions.

For the purposes of this study, the chromosomal data reported here have been combined with previously published observations on the chromosomes of *Cryptotermes cavifrons, Incisitermes milleri, I. schwarzi, I. snyderi, Neotermes castaneus,* and *N. jouteli* (Luykx and Syren 1979). The observations on the chromosomes of *Incisitermes minor, Neotermes luykxi, N. mona,* and *Pterotermes occidentis* are new. The observations on the chromosomes of *Mastotermes darwiniensis* Froggatt confirm these previously published by Bedo (1987).

Morphological characters were determined from preserved specimens in the collection of the U.S. National Museum of Natural History, Washington, D.C.

The morphological and allozymic data sets were analyzed, both separately and combined, with the PAUP (Phylogenetic Analysis Using Parsimony) package (versions 2.4 and Beta test 3.0) written by David L. Swofford (Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820). The morphological data were coded and analyzed as an ordered data set, with the transformation series based on outgroup comparison. The allozyme data were analyzed as an unordered data set. To ensure equal clustering power among characters with disparate numbers of states, the characters were weighted according to the number of states. Because each state has potential clustering power, a multi-state character has inherently more clustering power than a simple two-state character (Cranston and Humphries 1988). Therefore multi-state characters were down-weighted to be equal to two-state characters. Best estimates of relationship were obtained using both BRANCH SWAPPING (GLOBAL) and BRANCH AND BOUND subroutines for comparison.

Mastotermes darwiniensis was employed as the outgroup for the morphological analysis and the combined data analysis. No allozyme data were available for *M. darwiniensis,* so no outgroup was employed in the allozyme analysis. Instead, the allozyme tree was rooted at the midpoint and interpreted as an unrooted tree or network. Because a midpoint root is simply placed halfway between the two farthest points on a tree it does not affect character-state transformation series, and its removal results in a network.

Results

Morphology.—Thirteen morphological characters were examined, seven from imagoes and six from soldiers. When these characters were used for phylogenetic analysis, using *Mastotermes darwiniensis* as the outgroup, a single most-parsimonious cladogram was obtained (Fig. 1A). With the exception of *Neotermes castaneus,* the results are reasonably consistent with the taxonomy as reflected in the generic divisions. Examination of the morphological data matrix (Table 2) reveals that morphological characters are useful in indicating phylogenetic relations at the generic level, but (especially in the genera *Neotermes* and *Incisitermes*) are not generally useful in establishing phylogenies at the species level, nor even in distinguishing species within genera.

For most of the morphological characters examined, *Neotermes* species appear to be more similar than *Incisitermes* species to *Mastotermes darwiniensis* (family Mastotermitidae), the species used as the outgroup for the cladistic analysis. *M. darwiniensis,* because of several cockroach-like characteristics, is generally considered to be the species most similar to the original ancestors of modern termites (McKittrick 1965, Grassé 1986).

The morphology of *Neotermes castaneus*

Table 2. Morphological traits of some kalotermitid termites compared with *Mastotermes darwiniensis*. *Neotermes* species names: cas, *castaneus*; jou, *jouteli*; luy, *luykxi*; mon, *mona*. *Incisitermes* species names: mil, *milleri*; min, *minor*; sch, *schwarzi*; sny, *snyderi*; Pt. occ, *Pterotermes occidentis*; C. cav, *Cryptotermes cavifrons*; M. dar, *Mastotermes darwiniensis*.

Imago characters: 1: Left mandible, anterior margin of second marginal tooth (1) equal to or (2) longer than posterior margin of first marginal tooth; 2: Right mandible, posterior margin of second marginal tooth (1) equal to or (2) longer than molar plate; 3: Wing, median vein (1) weakly or (2) strongly sclerotized; 4: Wing, median vein (1) closer to radial sector than to cubitus, or (2) midway between radial sector and cubitus; 5: Wing, median vein (1) extends to tip unbranched, (2) or branched, or (3) joins radial sector at two-thirds length of wing; 6: Wing, veins (1) latticed apically or (2) not; 7: Foot (1) with or (2) without arolium.

Soldier characters: 8: Pronotum, shape of anterior margin, (1) concave or (2) incised; 9: Pronotum anterior margin (1) smooth or (2) serrated; 10: Pronotum, posterior margin (1) concave or (2) truncate; 11: Antennal segment no. 3, (1) similar to fourth, (2) greater than fourth + fifth, or (3) greater than fourth + fifth + sixth; 12: Eye pigment (1) absent, (2) slight, or (3) heavy; 13: Head shape (1) oval or pyriform, (2) elongate or reticulate, or (3) phragmotic.

Character Number	*Neotermes*				*Incisitermes*				*Pt. occ*	*C. cav*	*M. dar*
	cas	*jou*	*luy*	*mon*	*mil*	*min*	*sch*	*sny*			
Imagoes											
1. Left mand.	1	1	1	1	2	2	2	2	1	2	1
2. Right mand.	1	1	1	1	2	2	2	2	1	2	1
3. Wing vein sc.	1	1	1	1	2	2	2	2	2	1	1
4. Wing vein pos.	1	1	1	1	2	2	2	2	2	2	1
5. Wing m. vein	2	1	1	1	2	2	2	2	1	3	1
6. Wing v. latt.	1	1	1	1	2	2	2	2	2	2	1
7. Foot	1	1	1	1	1	2	1	1	2	1	1
Soldiers											
8. Pron. s. ant.	1	1	1	1	2	2	2	2	2	2	1
9. Pron. ant. m.	1	1	1	1	2	2	2	2	1	1	1
10. Pron. post.	1	2	2	2	2	2	2	2	1	1	1
11. Ant. segm.	1	2	2	2	2	3	3	2	2	1	1
12. Eye pigm.	1	3	3	1	1	2	2	2	1	1	1
13. Head shape	2	2	2	2	2	2	2	2	1	3	1

is generally similar to that of other species in the genus, but it differs from other *Neotermes* in three of the thirteen traits summarized in Table 2: in imago wing venation, in the relative length of the third antennal segment, and in the shape of the pronotum in soldiers (characters 5, 10, and 11). According to the results of the cladistic analysis (Fig. 1A), the last two of these traits are primitive traits retained from an ancestor (i.e. like the traits in the outgroup species), while the wing venation (character 5) is a derived trait similar to that in the genus *Incisitermes*. The cladogram suggests that the similarity of this trait in *Incisitermes* species and *Neotermes castaneus* is a result of convergent evolution.

Neotermes luykxi differs morphologically from *N. jouteli* only slightly. It is slightly smaller in size and has a somewhat narrower soldier postmentum (Nickle and Collins 1989). As described below, however, the two species can be reliably distinguished on the basis of allozyme patterns and chromosome number.

Allozymes.—The electrophoretic data are summarized in Table 3. Phylogenetic analysis of the allozyme data alone resulted in 7 equally parsimonious trees. These 7 trees could be combined via majority-rule con-

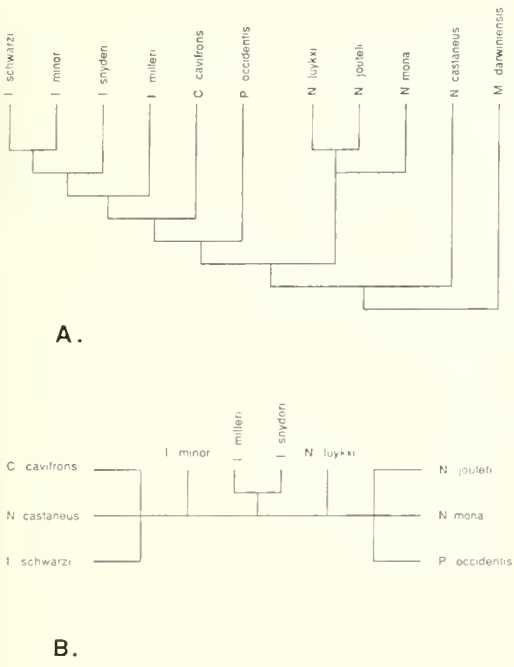

Figure 1

Fig. 1. Hypotheses of relationships based on independent analyses of the morphological and biochemical data. A. Cladogram based on the morphological data. It is the single most parsimonious hypotheses, with a consistency index (C.I.; Kluge and Farris 1969) of .708. B. Network based on allozyme data. The trichotomies are the result of seven most parsimonious trees (C.I. = .879) combined by the majority rule consensus method.

sensus to yield a single general hypothesis (Fig. 1B). It is clear that the morphological and allozyme results are not congruent (compare Fig. 1A with Fig. 1B). The morphology supports the monophyly of *Incisitermes*, the paraphyly of *Neotermes*, and the sister status of *N. jouteli* and *N. luykxi*. But the unrooted allozyme tree suggests that neither *Incisitermes* nor *Neotermes* are monophyletic, and does not support a *N. jouteli-luykxi* sister group.

However, combining data from several studies into a single matrix is often preferable to consensus methods for reconstructing phylogenies (Miyamoto 1985, Hillis 1987). Accordingly, the allozymic and morphological data were combined in a single matrix, and this resulted in a single most parsimonious cladogram (Fig. 2). The combined result is entirely congruent with the morphological result. In the combined cladogram all the nodes are well defined and all the terminal taxa are well delineated.

Of the 30 characters, 12 (1, 2, 4, 6, 8, 9, 14, 16, 17, 18, 24, and 25) were perfect fits (C.I. = 1.0; see legend to Fig. 1) to the final hypothesis (Fig. 2). Of these 12, only one character (24) had no synapomorphic content; the other 11 were all informative. The morphological characters were not good delineators at the species level: only 3 of the 10 taxa—*Cryptotermes cavifrons*, *Pterotermes occidentis*, and *Neotermes castaneus*—were delineated by any morphological characters, and even for these 3 taxa over half of the autapomorphies were allozyme characters. The rest of the taxa were identified as unique only by allozyme characters. (Every HTU (hypothetical taxonomic unit) node is, however, defined by at least one morphological character.)

The combined tree is in general agreement with the one presented by Krishna (1961, fig. 81) for the genera of the family Kalotermitidae, except for the position of *Pterotermes*, which is here joined with *Incisitermes* and *Cryptotermes* to form a monophyletic group, whereas Krishna put *Pterotermes* on a branch together with *Neotermes*.

The new species *Neotermes luykxi* could be distinguished from the morphologically similar *N. jouteli* at nine of the seventeen allozymic loci examined. This finding, along with the clear chromosome differences described below, leaves no doubt that the two are distinct species. Nevertheless, *N. luykxi* did appear most similar to *N. jouteli* among the other species examined by electrophoresis, being indistinguishable from it at eight of the seventeen loci studied. Three of these loci (characters 15–17: AC-C, ADH, and ALD) are synapomorphies for *N. luykxi* and *N. jouteli*, an additional two (characters 25

Table 3. Allozyme (enzyme) data obtained by starch gel electrophoresis on ten species of kalotermitid termites. For each locus, lower numbers indicate forms of the enzyme that migrated more slowly on the gels, higher numbers forms that migrated more rapidly. All enzymes were anodal, except for those designated "-C," which appeared on the cathodal side of the origin. 0 = enzyme not detected; X = not tested.

Species abbreviations as in Table 2.

AC, aconitase; ADH, alcohol dehydrogenase; ALD, aldolase; GAM, galactosaminidase; GK, glucokinase; GNDH, gluconate dehydrogenase; GPI, glucose phosphate isomerase; GR, glutathione reductase; LAP, leucine aminopeptidase; MDH, malate dehydrogenase; ME, malic enzyme; PEP, glycyl-leucine peptidase; PGM, phosphoglucomutase; SOD, superoxide dismutase; XDH, xanthine dehydrogenase.

Character Number	Locus	*Neotermes*				*Incisitermes*					
		cas	*jou*	*luy*	*mon*	*mil*	*min*	*sch*	*sny*	*Pt. occ*	*C. cav*
14.	AC	1	3	5	1	2	2	4	6	2	2
15.	AC-C	4	2	2	4	X	3	3	2	1	3
16.	ADH	0	2	2	1	X	0	4	5	3	6
17.	ALD	3	5	5	2	X	6	3	3	4	1
18.	GAM	1	1	1	1	2	3	4	3	0	3
19.	GK	6	1	3	3	4	5	6	3	4	2
20.	GNDH	2	4	1	5	6	1	7	6	3	2
21.	GPI	6	3	4	4	3	6	5	4	1	2
22.	GPI-C	2	2	1	2	1	3	4	1	2	1
23.	GR	4	3	2	1	2	2	2	0	3	3
24.	LAP	4	1	1	3	X	1	1	1	0	2
25.	MDH	1	6	6	6	4	7	4	2	5	3
26.	ME	2	2	2	1	5	6	3	4	5	3
27.	PEP	2	6	5	6	5	7	3	1	4	4
28.	PGM	6	4	5	4	5	3	5	5	1	2
29.	SOD	2	4	4	4	5	1	2	3	4	3
30.	XDH	1	2	3	1	4	3	2	3	0	3

and 29: MDH and SOD) are synapomorphic for the group that includes *N. mona*, and the remaining three (characters 18, 24, and 26: GAM, LAP, and ME) appear to be primitive characters shared by other species as well.

Chromosomes.—*Neotermes luykxi* and *N. jouteli* can be readily distinguished on the basis of their chromosomes (Figs. 3e, f). Not only are the chromosome numbers different (2n = 45 and 56, respectively), but the N.F. ("nombre fondamental," the number of major chromosome arms) is different also (haploid, 25 and 28, respectively). Furthermore, *N. luykxi* populations have a sex-trivalent; no sex-multivalents of any kind have been seen in *N. jouteli*.

The results of the chromosome study for all species are summarized in Table 4; several examples are illustrated in Fig. 3. The karyotypes of the ten kalotermitid species examined for this study show considerable variation. Diploid chromosome numbers range from 28 (*Incisitermes milleri*) to 79 (*Pterotermes occidentis*). The diploid chromosome sets of some species are composed entirely of acrocentrics, while others contain, in addition to acrocentrics, from 3 to 22 metacentrics. Some species are without morphologically differentiated sex chromosomes, while others have multiple sex chromosomes that in male meiosis form chains or rings containing from 3 to 14 chromosomes.

The total number of major chromosome *arms* (the "nombre fondamentale," N.F.) in different species shows relatively little variation compared to the chromosome number itself (see Table 4). For example, the haploid chromosome numbers of *Incisitermes schwarzi, N. mona*, and *N. jouteli* are 16, 23 and 28, respectively, while the total num-

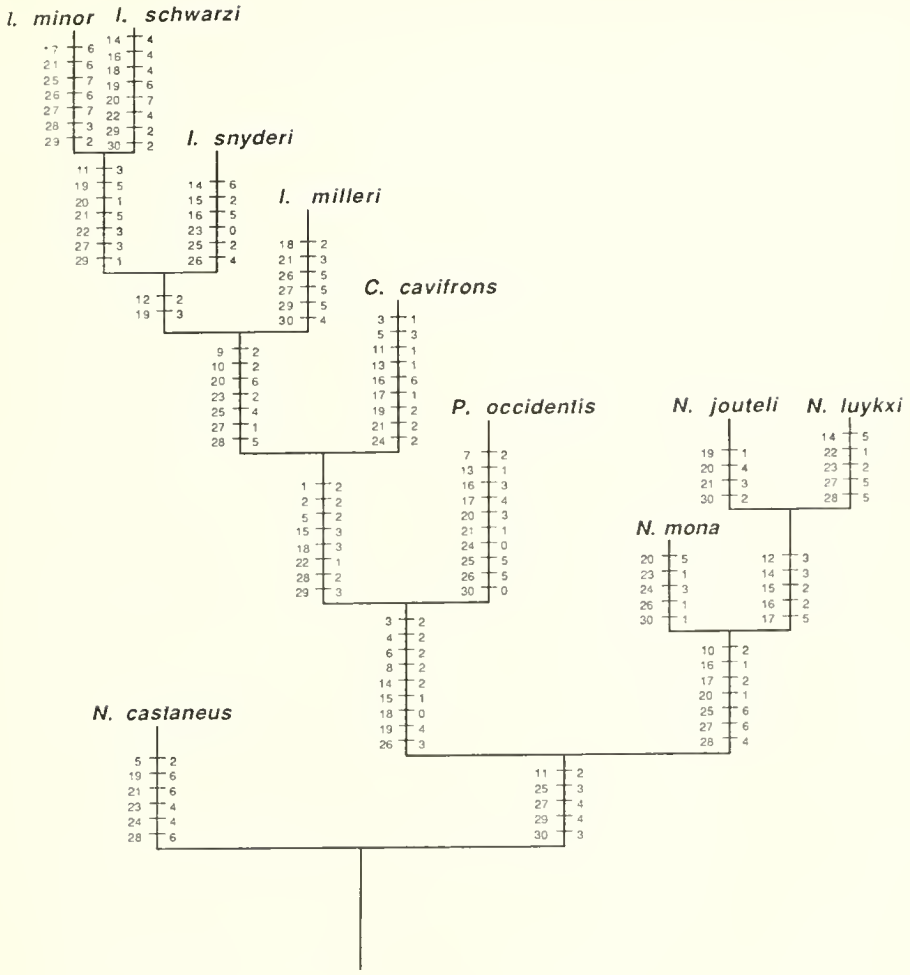

Figure 2

Fig. 2. The final cladogram constructed from the combined morphologic and allozymic matrix. Excluding uninformative characters, the C.I. is .780. The steps associated with the branch connecting the outgroup to the most recent common ancestor of the study group are not shown because they are unimportant in defining the relationships of the study group. Numbers to the left of the hash marks represent characters; numbers to the right of the hash marks represent character states.

bers of major chromosome arms for these species are 27, 27, and 28.

When the total numbers of major chromosome arms are compared among the different species, the numbers appear to fall into distinct groups. *I. milleri* has N.F. = 14; most of the other *Incisitermes* and *Neotermes* species have an N.F. ranging from 25 to 28; and *Pterotermes occidentis* and *Mastotermes darwiniensis* have N.F. = 49 and 52, respectively.

It is possible to order the chromosome changes in plausible evolutionary sequences, assuming for example that the N.F. changes from low to high by some sort of amplification process, that centric fusions increase the number of metacentric chromosomes at the expense of acrocentric chro-

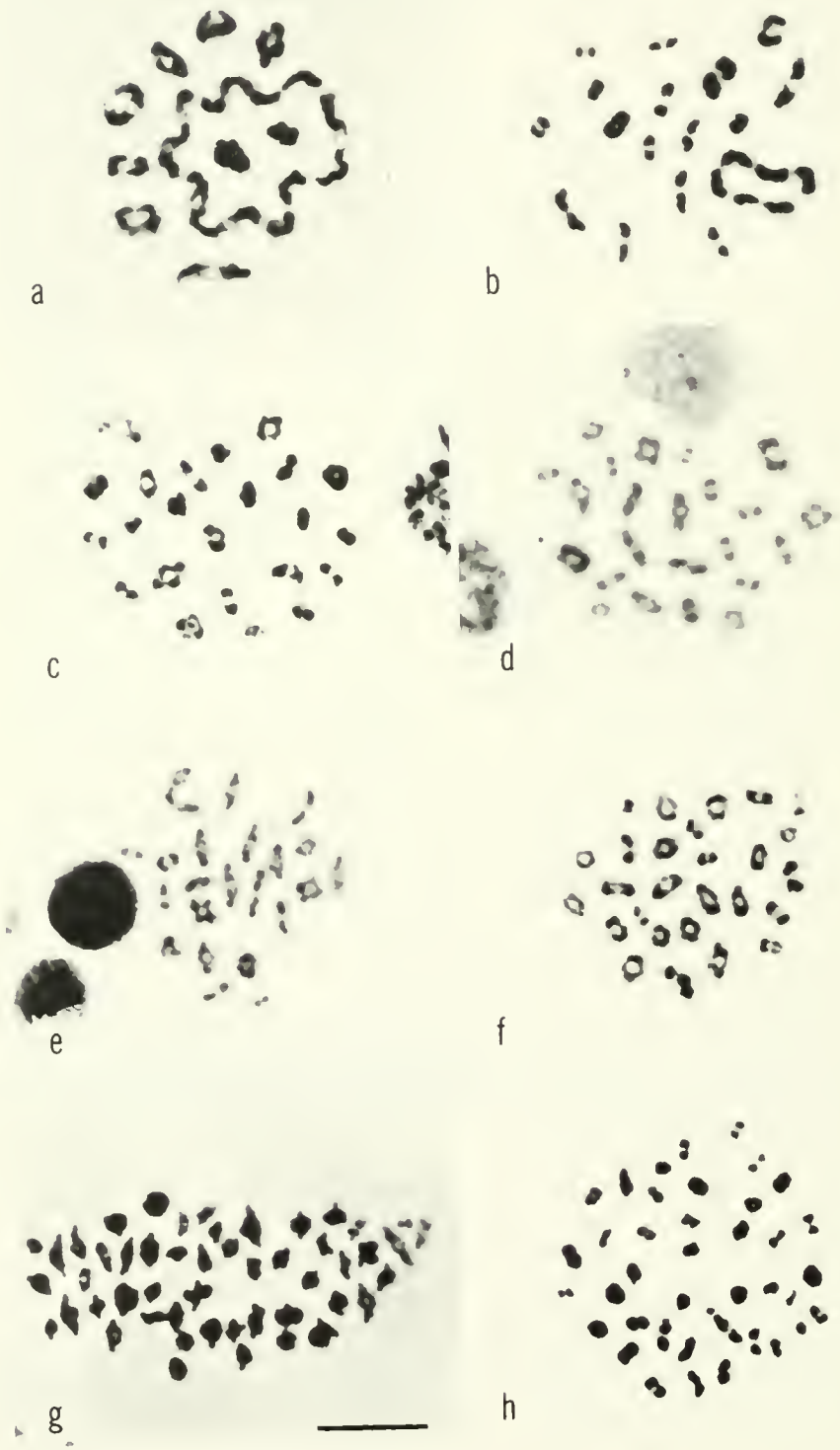
a
b
c
d
e
f
g
h

Table 4. Chromosomes of several species of kalothermitid termites and of *Mastotermes darwiniensis*.
The columns in the table are: *a*, species name; *b*, the reference for the karyotype (1, this report. 2, Luykx and Syren 1979; 3, Bedo 1987); *c*, diploid chromosome number in males; *d*, approximate number of metacentric (two-armed) chromosomes in the diploid set; *e*, the N.F. ("nombre fondamental," or total number of chromosome arms) of the haploid set; *f*, the number of recognizable sex chromosomes (usually multivalent).

a Species	*b* Ref.	*c* 2n	*d* Meta	*e* N.F.	*f* Sex Chrom.
Neotermes castaneus	2	38	14	26	VI
Neotermes jouteli	2	56	0	28	—
Neotermes luykxi	1	45	3	25	III
Neotermes mona	1	46	8	27	—
Incisitermes milleri	2	28	0	14	—
Incisitermes minor	1	37	11	25	III
Incisitermes schwarzi	2	32	22	27	XIV
Incisitermes snyderi	1, 2	45	8	27	I
Pterotermes occidentis	1	79	17	49	III
Cryptotermes cavifrons	2	40	2	21	—
Mastotermes darwiniensis	1, 3	98	6	52	—

mosomes, and that a simple sex-chromosome pair is built up to multivalent rings and chains by means of successive centric fusions and translocations between sex chromosomes and autosomes. On such assumptions plausible phylogenies based on chromosomal changes alone can be constructed; an example is illustrated in Fig. 4.

It is clear that this phylogeny bears little relation to that based on morphology and allozymes (compare Fig. 4 with Figs. 1 and 2). As explained in the Discussion, there is reason to think that *chromosomal changes* may occur more frequently and become established in populations more rapidly than the *genic changes* that accompany speciation and that are reflected in the morphological and allozymic variation between species. Therefore the chromosomal data were not added to the allozymic and morphological data matrix, and no attempt was made to arrive at a consensus phylogeny using the chromosomal data.

Discussion

One of the reasons for undertaking this study was to clarify the systematic relationship of a new termite discovered in south Florida in 1984. Initially thought to be simply a size variant of *Neotermes jouteli*, it became the subject of a careful morphometric study (Nickle and Collins 1989) when it was later found to have a chromosome number different from that of *N. jouteli*. On the basis of the morphometric study (Nickle and Collins 1989), it was recognized as a distinct species and named *Neotermes luykxi*. The present study established clearly that, on the basis of both chromosome number and enzyme differences, it is a species distinct from *N. jouteli*.

A difference in chromosome number alone is not sufficient to establish species status. "Chromosomal races" of the same species may also have different chromosome numbers as a result of variation in the number of centric fusions (John 1983). But

←

Fig. 3. Male meiosis in several lower termites. Magnification is approximately the same for all cells, about 1400×. Bar = 10 μm. a, *Incisitermes schwarzi*, 9 bivalents and a sex-multiple of 14 chromosomes; b, *Neotermes castaneus*, 16 bivalents and a sex-multiple of 6 chromosomes; c, *Incisitermes snyderi*, 22 bivalents and a sex-univalent, upper left; d, *Neotermes mona*, 23 bivalents; e, *Neotermes luykxi*, 21 bivalents and a C-shaped sex-trivalent, at top; f, *Neotermes jouteli*, 28 bivalents; g, *Mastotermes darwiniensis*, 49 bivalents; h, *Pterotermes occidentis*, 38 bivalents and a linear sex-trivalent, just below and to the right of center.

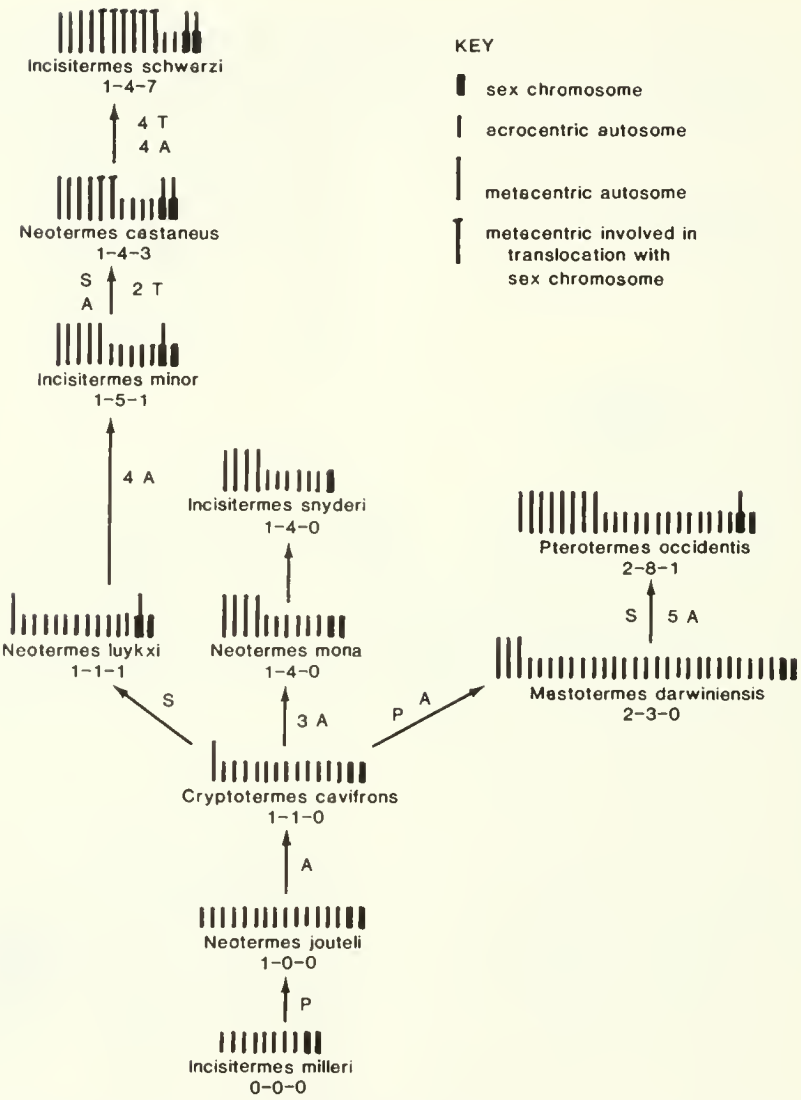

Fig. 4. Schematic representation of ordered karyotype changes in 11 species of lower termites (10 Kalotermitidae, 1 Mastotermitidae), based on the data in Table 4. Arrows are labeled by the following karyotypic changes: P, polyploidization; A, autosomal centric fusion; S, sex-chromosome-autosome centric fusion; T, translocation between autosome and sex-chromosome. The 3-digit formula under each species name indicates for each karyotype (ploidy level)–(haploid number of autosomal metacentrics)–(haploid number of sex-chromosome metacentrics). This tree was constructed by hand, minimizing genome amplification events and avoiding centric fissions on the assumption that these are much less frequent than centric fusions and translocations in karyotype evolution. This and other parsimonious trees of karyotype evolution (constructed by PAUP) are not congruent with the trees (Figs. 1 and 2) derived from morphological and allozyme characters (see text).

in such cases the N.F., the number of major chromosome arms, is the same for all races. This is not the case here; the haploid N.F. for *luykxi* is 25, while that for *jouteli* is 28. This indicates that the two types are not simply different populations of a single polytypic species related by centric fusions. Moreover, fusions between autosomes and sex chromosomes have occurred in *luykxi* but are so far unknown in *jouteli*.

These chromosomal differences, along with the enzyme differences described in this

paper (9 out of 17 loci studied) and the slight but definite morphological differences described by Nickle and Collins (1989), leave little doubt that *luykxi* and *jouteli* do not share a common gene pool, and are therefore different species. The phylogenetic relationships of the two species, as reflected in the cladogram based on the combined morphological and electrophoretic data (Fig. 2), indicate that the two species are nevertheless closely related, and therefore *luykxi* is appropriately included in the genus *Neotermes*.

The cladogram (Fig. 2) is based on 13 morphological characters and 17 enzyme characters. It might be argued that the relatively small number of individuals sampled in the electrophoretic studies could bias the cladogram, if numerous enzyme polymorphisms went undetected, and apparently fixed differences between species were in fact simply different allelic forms uncovered as a result of chance sampling among a small number of genomes.

For several reasons, it is unlikely that many of the species differences represent simply allelic differences in polymorphic populations, and that the phylogenetic tree topology is thereby significantly biased. First, levels of enzyme polymorphism in the lower termites are probably low. In the only kalotermitid species studied extensively to date, *Incisitermes schwarzi*, Santos and Luykx (1985) found only 4 polymorphic loci out of 23 studied (17%). Limited though the samples of each species in the present study were, there were no other clear cases of intraspecies polymorphism, indicating that levels of polymorphism in the other species are generally low also.

Secondly, when 4 genomes are sampled for each species (the minimum number sampled for each species in this study), the probability that two species will appear to have fixed differences when in fact they both are polymorphic at a given locus, is not very high. It can be calculated, for example, that if two species are both polymorphic at a locus, and alternate alleles each occur at a frequency of .95 in the two different species, then the probability is .66 that, when 4 genomes are sampled from each species, one species will appear to be fixed for one allele and the other species will appear to be fixed for the other allele. This means that under these special circumstances—approaching a state of fixed species differences—about ⅔ of the truly polymorphic loci will show up as fixed differences in the two species; that is, only about 2 loci out of the 17 loci studied, assuming that *Incisitermes schwarzi* is fairly representative of the family (see above). If the two alleles are both equally frequent at a given locus in each of two species, the probability is less than 1% that the two species will appear to be fixed for the different alleles.

Finally, it has been shown that when a relatively large number of loci are used, and the fraction of loci that are polymorphic is relatively low (as appears to be the case here), samples as small as even single individuals from each species give cladogram topologies that are not any different from those obtained when larger species samples are used (Hillis 1987; see also Gorman and Renzi 1979).

Admittedly, larger sample sizes for each of these species would resolve these questions. But the above considerations make it improbable that failure to detect enzyme polymorphisms because of limited sample sizes significantly affected the topology of the cladogram.

The cladogram presented in Fig. 2, combining both morphological and electrophoretic data, was rooted using *Mastotermes darwiniensis* as the outgroup. Samples of this species were unfortunately not available at the time of the electrophoretic studies, so the rooting of the tree is based on the morphological data alone. In view of the general agreement (similar consistency indices) between the morphological and electrophoretic data, however, it seems unlikely that the addition of electrophoretic data from *Mastotermes* would significantly alter the topology of the tree. This is a point that

can be investigated more thoroughly in future studies.

The phylogeny as presented in Fig. 2 is in general agreement with that proposed by Krishna (1961) on the basis of classical morphological studies. There are, however, two differences. The first is that *Pterotermes occidentis* is phylogenetically related to the *Incisitermes-Cryptotermes* branch of the kalotermitids, not to the *Neotermes* branch as Krishna supposed. The association of *P. occidentis* with *Incisitermes* and *Cryptotermes* rather than *Neotermes* is supported by 9 derived characters, 7 of which are shared with at least one other species of *Incisitermes*, and 3 of which are shared with all the *Incisitermes* species studied. These numbers make it highly improbable that *Pterotermes* is more closely related to *Neotermes* than to *Incisitermes* (see Felsenstein 1985).

The second difference with Krishna's phylogeny is that *Neotermes* appears to be paraphyletic. *Neotermes castaneus* (unfortunately the type species for the genus) in fact appears in Fig. 2 as a sister group to the other *Neotermes* species and to *Incisitermes* species. The data indicate that some revision of the taxonomy of this branch of the Kalotermitidae is required, but it seems premature to revise it until more extensive studies, including more members of the genus, are carried out.

It is interesting that the morphological characters and allozymic characters appear to define phylogenetic groupings at different levels: species are defined more by their unique allozyme characters than by their morphology, while the morphological characters tend to define higher taxa (genera). This tendency has also been observed in other groups of animals (e.g. see fig. 4 in Hillis 1987). The observation suggests that allozymic changes frequently accompany speciation, while morphology is more conserved—a tendency that might be expected if single base changes are responsible for allozyme differences, while significant morphological differences require more extensive genetic repatterning.

Some investigators (e.g. Miyamoto 1983) have treated the karyotype as a single character with multiple states (arising from centric fusions, pericentric inversions, etc.), and have combined karylogical data with the morphological and electrophoretic data to generate phylogenetic trees. Treating chromosomal data in this way, however, assumes that chromosomal changes occur at approximately the same rates and play approximately the same role in speciation as do the gene mutations that lead to changes in morphology and allozymes. Rates of structural changes in chromosomes, however, are several orders of magnitude higher than rates of gene mutations (Jacobs 1981, Van Dyke et al. 1983, Hook et al. 1984). The role of chromosomal changes in speciation is still a controversial subject (e.g. Sites and Moritz 1987), and it therefore seems better to treat chromosomal changes separately, and not combine them with morphological and allozyme data.

It is theoretically possible to construct a separate phylogeny based on the chromosomes of the ten kalotermitid species studied here and of *Mastotermes darwiniensis* (Fig. 3). As outlined in the following paragraphs, the changes that have apparently led to the karyotypic differences between these species are (i) an increase in number of major chromosome arms, possibly by a process akin to polyploidization; (ii) centric fusion between autosomal acrocentrics; (iii) centric fusion between sex chromosomes and autosomes; and (iv) whole-arm translocation between autosomal and sex-chromosomal metacentrics.

Evolutionary polyploidization in animals is very rare (White 1973), and it is uncertain whether this process has really occurred in these termites. But the numbers of major chromosome arms (N.F.) in the species studied here seem to fall into distinct categories: *Incisitermes milleri* has N.F. = 14, most of the other *Incisitermes* and *Neotermes* species have N.F. ranging from 25 to 28, and *Pterotermes occidentis* and *Mastotermes darwiniensis* have N.F. = 49 and

52, respectively. This is almost a doubling series and suggests, if not polyploidization, at least distinct evolutionary episodes of amplification.

The karyotypes of many of these termite species consist of mixtures of acrocentric and metacentric chromosomes. As would be expected if centric fusions or fissions were important in the karyotypic changes exhibited by these termites, metacentric chromosomes are in general about twice the size of acrocentric chromosomes. And even if the absolute chromosome numbers differ, species with similar N.F. have similar DNA contents. The haploid DNA content of *Neotermes jouteli* is 1.30 pg, almost identical with that of *Incisitermes schwarzi*, 1.35 pg (Luykx, unpublished data). While the haploid chromosomes numbers of these two species are quite different, *N. jouteli* with n = 28 (all acrocentrics) and *I. schwarzi* with n = 16 (5 acrocentrics and 11 metacentrics), the N.F. for these two species is almost the same (28 and 27, respectively). Differences in chromosome number are probably due primarily to centric fusions rather than centric fissions, since fusions are much more common than fissions among orthopteroid insects in general (Hewitt 1979), and because there is little doubt that fusions are responsible for the origin of the sex-trivalents in *Neotermes luykxi, Incisitermes minor,* and *Pterotermes occidentis,* as well as in other kalotermitid species (Luykx and Syren 1979).

The formation of the multivalent rings seen in male meiosis in *Neotermes castaneus* and *Incisitermes schwarzi* can be accounted for by a series of whole-arm translocations between autosomal and sex-chromosomal metacentrics. Starting with a metacentric pair of sex chromosomes (which may themselves have arisen by centric fusions), each successive translocation of a sex chromosome with an autosome would increase the size of the sex-multivalent by two chromosomes (Syren and Luykx 1981). Thus, one translocation would give a ring of 4 chromosomes, an additional translocation would give a ring of 6, and so on. Evidently, two such translocations have occurred in *N. castaneus*, and a total of 6 such translocations have occurred in the *I. schwarzi* population used in these studies (see Luykx and Syren 1979 and Luykx 1987 for other translocation variants in this species).

It seems likely that a karyotype consisting entirely of acrocentric chromosomes was the ancestral condition. This karyotype is the most common one among the kalotermitids (Luykx and Syren 1979, Luykx 1990). The chromosomal variations seen in these termites, then, in accord with the considerations discussed above, can be understood as arising from a limited number of processes acting on a primitive all-acrocentric karyotype: the amplification of the number of chromosome arms (perhaps by polyploidization-like events), the fusion of centromeres (between autosomes and sex chromosomes as well as among autosomes), and the translocation of whole arms between autosomal and sex-chromosomal metacentrics.

A phylogeny of chromosome changes, based on the data in Table 4, can be constructed on the above principles. A simple phylogeny is shown in Fig. 3. It is obvious that this and other parsimonious trees of karyotype evolution (constructed by PAUP) bear little relation to the cladogram derived from morphological and allozyme characters (Fig. 2). The most reasonable explanation for the discrepancy is that chromosome arrangements in these insects are too labile to be good indicators of phylogeny. In other words, chromosome changes may arise and be fixed in populations more rapidly than the speciation events themselves, a view supported by the extensive karyotype variation also observed *within* these species (Syren and Luykx 1981, Luykx 1983, Luykx 1987).

Similar karyotype modifications may therefore occur independently on separate branches of the "true" phylogeny (here assumed to be approximated by Fig. 2). Thus,

since there is no obvious mechanism for halving genome size in a single step, discrete genome amplification events (polyploidization?) would have to have occurred separately on all branches except the one leading to *Incisitermes milleri*. Autosomal centric fusions appear to have occurred to varying extents on different branches, giving the same number of autosomal metacentrics in *Incisitermes snyderi* and *Neotermes mona*, for example, quite independently. Similarly, frequent centric fusions and repeated translocations between metacentric sex chromosomes and metacentric autosomes, to give multivalent rings in male meiosis, appear to have occurred independently on separate branches leading to *Neotermes castaneus* and *Incisitermes schwarzi*.

It seems likely that these processes of karyotype modification—approximate doubling of chromosomal material, centric fusion, and whole-arm translocations—are all widespread and common enough that virtually every lineage is subject to them. The different karyotypes that are currently observed in these various species are therefore probably simply the outcome of variations in the frequency with which these chromosome changes occur within lineages, and in population factors that affect the likelihood that the changes will be fixed.

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NEW SPECIES OF BUPRESTIDAE (COLEOPTERA) FROM THE DOMINICAN REPUBLIC

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Abstract.—Three species of Buprestidae are newly described, illustrated, and distinguished from other Antillean and closely related species in their respective genera: ***Sambomorpha clarki***, ***Agrilus klapperichi***, and ***Neotrachys bilyi***. Additional records are given for *Acmaeodera cruenta* (Olivier), *Chrysobothris haitiensis* Fisher, *Taphrocerus haitiensis* Fisher, *Leiopleura darlingtoni* Fisher and *L. gibbipennis* (Fisher). A list of Hispaniolan Buprestidae is given in a table.

Key Words: *Agrilus*, biogeography, distribution, Hispaniola, *Neotrachys*, *Sambomorpha*

Recent collections, primarily in the Dominican Republic, show the buprestid fauna of Hispaniola to be relatively poorly known, especially for smaller species. This paper describes three new species, reports recent collections of previously described species, and gives a checklist of forms currently known to occur on the island. Additional specimens in the Mastogeninae have been seen but remain undetermined.

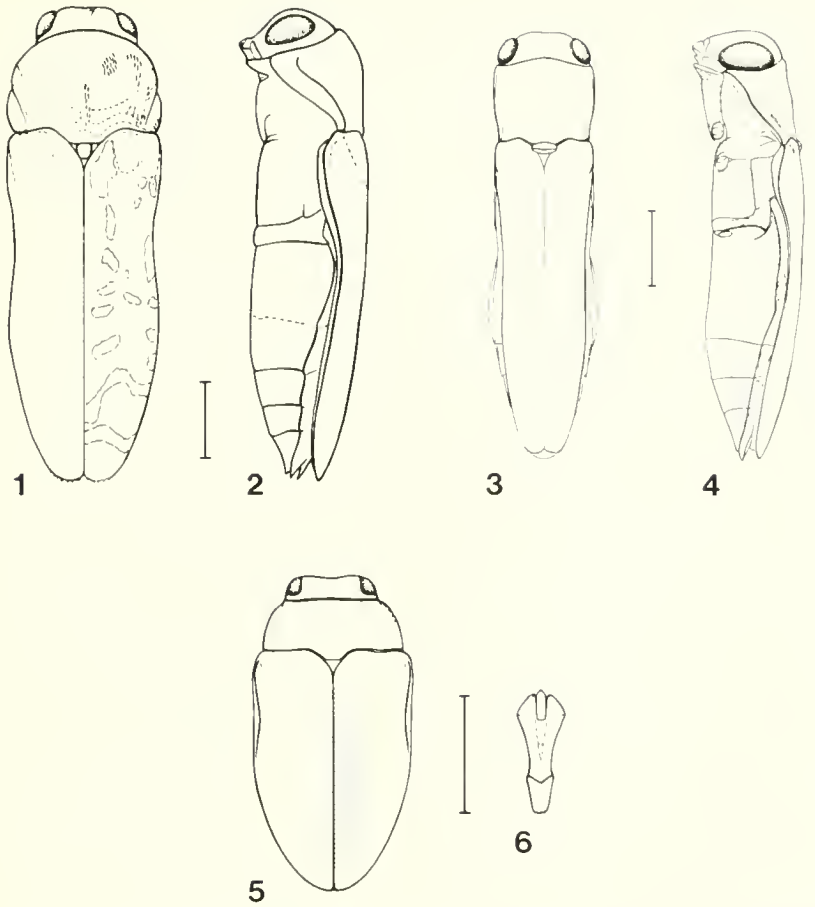
The following species appear not to be described:

Sambomorpha clarki, NEW SPECIES
(Figs. 1, 2)

Description.—Holotype, probably female: Length 6.4 mm, width 2.1 mm; dorsoventrally somewhat flattened, strongly so above; moderately shining; head, pronotum and scutellum purplish red, darker on pronotum postero-medially, more aeneous on anterior angles, elytra dark reddish purple, more reddish at base and on margins; pronotum ornamented with patches of elongate white setae in anterior and posterior angles, along basal ½ of midline and in spots on anterior margin ⅓ the distance to margin, elytra ornamented with white setae in a broken line of spots on either side of suture and along lateral margin on basal ⅔ and in two irregular transverse fascia at apical ¾ and near apex; otherwise with long, thin, dark setae; beneath purplish with golden reflections.

Head with front shallowly depressed along midline, with indistinct convexities on either side of midline at middle of eye; surface nearly smooth on dorsal ½, especially medially, weakly rugose on ventral ½; sparsely clothed with long white setae dorsally, with shorter, denser setae along midline on ventral ½; epistoma narrow between antennae, faintly carinate along midline to base, angulately emarginate along base; antennae reaching only anterior ⅓ of pronotal length, serrate from the fifth segment, outer joints rounded-triangular; eyes small, broadly oval, wider ventrally.

Pronotum 1⅔ wider than long, widest just anterior to base; sides slightly sinuate then narrowed to apical angles, posterior angles narrowly rounded-obtuse; when viewed from side lateral margin sinuate, strongly produced, especially for anterior ½; anterior margin broadly rounded; base with narrow, smooth margin, angulate-emarginate at



Figs. 1–6. Figs. 1, 2. *Sambomorpha clarki*, n. sp.; line equals 1 mm. 1, dorsal view. 2, lateral view. Figs. 3, 4. *Agrilus klapperichi*, n. sp.; line equals 1 mm. 3, dorsal view. 4, lateral view. Figs. 5, 6. *Neotrachys bilyi*, n. sp. 5, dorsal view, holotype—shading indicates area of dark violet; line equals 1 mm. 6, genitalia, allotype; line equals 0.5 mm.

middle of each elytron, median lobe moderately produced and truncate in front of scutellum; disk broadly convex anteriorly, transversely depressed on each side at base, strongly so interior to prehumeral carinae to anterior angles; prehumeral carinae very strong, parallel to lateral margin, extending from basal margin nearly to anterior margin of pronotum; narrowly depressed between carina and margin; surface somewhat finely imbricate-punctate, intervals smooth. Scutellum nearly flat, smooth.

Elytra slightly wider than pronotum at base; sides shallowly constricted then slightly expanded to middle, then gradually narrowed to broadly, separately rounded and denticulate tips; sides of abdomen slightly exposed above; disk strongly flattened, with rather strong transverse basal depressions; surface finely imbricate-punctate.

Prosternum confluent-punctate, uniformly, sparsely clothed with long, white, recumbent setae, deeply transversely depressed at base of prosternal lobe, which is declivous and broadly, arcuately emarginate; sides of prosternal process converging gradually to behind coxal cavities, then acutely angulate. Abdomen convex ven-

trally, marked with transverse crenulate lines; sparsely, uniformly clothed with fine, white, recumbent setae, and small spots of denser setae on anterio-lateral portions of segments 2–4; suture between first and second segments indicated only at sides; last segment broadly, shallowly emarginate at apex. Tibiae nearly straight, armed with a small, thin spine on inner margin at apices; anterior tibiae denticulate on outer margin at base. Tarsal segments equal; tarsal claws similar on all feet, cleft at base, inner tooth straight, much shorter than outer one.

Holotype.—Rep. Dominicana, Bani, 30.IX.1985, W. E. Clark, to be deposited in USNM.

The genus *Sambomorpha* was described by Obenberger (1924) for a single species from southeastern Brasil. All members of the genus most obviously share the dorsoventrally depressed body form, strong and sinuate prehumeral carinae on the pronotum, and similar diffuse patterns of pubescence on the elytra. I have recently (Hespenheide 1979) transferred to the genus a second Brasilian species described originally as an *Agrilus*, and have seen undescribed material from Mexico. *Sambomorpha clarki* can be distinguished from both Brasilian species by the absence of a posthumeral carina on the elytra, color, and somewhat larger size; and from the Mexican forms by its color and more definite pattern of pubescence on the elytra. *Sambomorpha* shares its rather widely disjunct and unusual distribution in the New World (Hispaniola, Mexico, southeastern Brasil), presumably a relictual one, with the genus *Tetragonoschema*. *Cyphothorax* shows a similar disjunct range between Mexico and southeastern Brasil. The type appears to be a female, although it was not dissected.

Agrilus klapperichi, New Species
(Figs. 3, 4)

Description.—Holotype female: Length 5.9 mm, width 1.4 mm; moderately elongate and robust, strongly flattened above; weakly shining, black, head, sides of pronotum, and ventral surfaces with bronzy reflections; elytra ornamented with five pairs of small pubescent spots.

Head with the front wide, a small transverse depression below middle and a narrow one along midline above and below middle, lateral margins nearly straight; surface moderately rugose, clothed with moderately long setae which radiate from the central depression, becoming very short on occiput; epistoma moderately wide between the antennae, shallowly emarginate along base; antennae serrate from the fourth segment, outer joints triangular; eyes about equally rounded above and below.

Pronotum slightly wider than long, subequal at base and apex, widest at apical ¼; sides subparallel at base, shallowly convex to apical angles; posterior angles nearly perpendicular; when viewed from side marginal and submarginal carinae narrowly separated for their entire length, more broadly so at apex, weakly sinuate; anterior margin sinuate, median lobe moderately produced and broadly rounded; base angularly emarginate at middle of each elytron, median lobe slightly produced and weakly emarginate in front of scutellum; disk shallowly convex, depressed on each side at base, strongly so at anterior angles, two shallow transverse medial depressions and depressed along midline for basal ½; prehumeral carinae subparallel with and narrowly separated from lateral margin, extending for basal ½ of pronotum; surface rather finely, transversely rugose, impunctate, setae short and inconspicuous on disc, longer and more conspicuous just interior to prehumeral carinae and lateral margins. Scutellum strongly transversely carinate, surface shagreened.

Elytra subequal to pronotum at base, widest at humeri; sides very shallowly constricted and then slightly widened to apical ⅓, then gradually narrowed to tips, which are separately rounded and finely toothed; sides of abdomen exposed dorsally; disk with moderate basal depressions and shallowly

depressed along sutural margins, except just behind scutellum; surface rather finely imbricate-punctate, uniformly clothed with short setae, each elytron ornamented with five small round spots of denser setae: in basal depression, along suture at basal ⅓, ⅔, and near apices, and near sides just beyond middle.

Posterior coxae nearly straight on posterior margin. Abdomen with suture between first and second segments distinctly indicated at sides; anterior vertical portions of segments 2, 3, and 4 ornamented with oval spots of longer setae; dorsal portions of segments 1, 3, and 4 densely setose. Tibiae unarmed. Posterior tarsi shorter than tibiae, first joint subequal to following three united. Tarsal claws similar on all feet, cleft with inner tooth subparallel to and shorter than outer one.

Holotype.—Rep. Dominicana, Bani, 30.IX.1972, J. & S. Klapperich (Basel).

Agrilus klapperichi is quite different from the other, much larger species of *Agrilus* (*A. dominicanus* Thomson, related to *A. macer* LeConte) known from Hispaniola (Fisher 1925). *A. klapperichi* appears to be related to the group of species that in the United States includes *A. obsoletoguttatus* Gory, *A. exsapindi* Vogt, *A. limpiae* Knull, *A. scitulus* Horn and *A. taeniatus* Chevrolat. Among Central American species, *A. klapperichi* appears most closely related to *A. simulans* Waterhouse, *A. femoralis* Waterhouse and *A. antennatus* Waterhouse. All of these species are characterized by similar patterns of pubescence on the elytra and ventral body surfaces and by sexual dimorphism in the antennae, in which males tend to have antennae which are relatively more elongate and occasionally modified otherwise. The characters which are unique to *A. klapperichi* compared to the North and Central American species mentioned above are (a) the prehumeral carina subparallel with the marginal carina, (b) the separation of the marginal and submarginal carinae of the pronotum for their entire length, and (c) the transverse medial depression on the front. Because the specimen is mounted venter down on a card, characters on the ventral surface could not be described.

Neotrachys bilyi, New Species
(Figs. 5, 6)

Holotype female.—Length 2.75 mm, width 1.3 mm; oval, moderately convex, rounded-quadrate in front, attenuate posteriorly; inconspicuously short pubescent; moderately shining and strongly shagreened; head, pronotum and humeri greenish blue, elytra blue, becoming dark violet blue on inner apical ½ along suture and beyond basal ⅓; beneath black.

Head depressed on front along midline between eyes and with transverse depression between epistomal pores; epistomal pores moderate in size; surface moderately densely ocellate-punctate, punctures less dense and finer between eyes; intervals shagreened; epistoma with anterior margin very shallowly angulate-emarginate; subocular pores large; antennae with 6th segment slightly produced below, conspicuously serrate only from 7th segment.

Pronotum moderately convex, about 2½ times as wide as long, distinctly narrower in front than behind, widest at base; sides arcuately rounded from base, more strongly so at anterior angles, narrowly margined; anterior angles obtuse; posterior angles perpendicular; anterior margin nearly transverse, with obsolete lobe at middle; posterior margin transversely feebly sinuate with strong subtruncate median lobe before scutellum; surface shallowly depressed along basal margin and more strongly so at anterior angles; rather densely ocellate-punctate along margins, more densely so in posterior angles, more finely, simply and less densely so on disk; intervals strongly shagreened. Scutellum small.

Elytra moderately convex, wider than pronotum at base; humeral angles broadly rounded-quadrate; sides nearly parallel to middle, then shallowly attenuate to con-

jointly, rather narrowly rounded tips; each elytron with small, shallow depression at base interior to humerus, a deep, narrow, elongate one behind humerus along lateral margin, and an elongate, shallow one along suture for posterior ⅔; surface regularly punctate, intervals strongly shagreened.

Prosternum sparsely, faintly ocellate-punctate, intervals smooth, greenish-blue; anterior margin shallowly arcuate; prosternal process moderately broad, broadened slightly behind coxal cavities, and broadly, rounded-quadrate at apex. Hind coxae depressed along their length, broadly, shallowly biemarginate with broadly, obtusely rounded projection dorsal to attachment of hind legs. Abdomen beneath with dense, large, shallow, fine ocellate punctures, which are elongate and denser at base and sides of first segment, sparser and more rounded on segments 2–5; intervals densely, finely, obsoletely reticulate-striolate.

Allotype male: Similar to female, except bright golden-green above, with darker golden coppery reflections on top of head, disk of pronotum, and central portions of each elytron.

Holotype.—Rep. Dominicana, Cazabita, 1250 m, 15.VIII.1972, J. & S. Klapperich (Basel).

Allotype.—Dominican Rep., La Vega, 15 km E of El Rio, 26.V.1978, C. W. & L. B. O'Brien & Marshall (USNM).

Neotrachys bilyi differs strikingly in appearance from most other Antillean *Neotrachys* treated in the revision of the genus (Hespenheide 1980). Although proportioned like *N. dominicanus, N. fennahi* and *N. guadeloupensis*, it is conspicuously shagreened (or granular reticulate) like *N. hoffmani*. The color of the holotype, that is, greenish-blue anteriorly shading to deep violet-blue on the inner posterior portions of the elytra, is unique among the Antillean species. The male is less strikingly colored and is similar to some individuals of *Neotrachys* from Puerto Rico. It is not clear whether these latter specimens represent *N. hoffmani*, in which case that species is more variable than originally treated, or whether they belong to a second, undescribed Puerto Rican species; additional specimens are needed to determine which is the case. *N. bilyi* can be separated from these questionable forms as follows:

	N. bilyi	*N. (hoffmani?)*
dorsal setae	minute	conspicuous
subocular pores	large	inconspicuous
pronotum	broader, shorter	narrower, more elongate
elytral intervals	strongly shagreened	mostly smooth
posterior margin, hind coxae	biemarginate	nearly straight
distribution	Hispaniola	Puerto Rico

N. bilyi is readily distinguished from typical *N. hoffmani*, which are strongly depressed along the lateral margins of the elytra near the middle and dark olive green in color. The characteristics in the table separate *N. bilyi* from all Central American species as well (Hespenheide 1982).

The beetle is named in honor of Svatopluk Bílý, who allowed me to see and describe this and the preceding species.

The following species are represented by additional distributional data:

Acmaeodera cruenta (Olivier)

Specimens examined.—Dominican Republic: 6.5 mi W Azua, 13.VI.1968, H. A. Hespenheide, on *Prosopis* (RLWC); Peravia, 6 km W Bani, 4, 15.IX.1983, W. E. Clark (AUBU, CHAH).

Chrysobothris haitiensis Fisher, 1930:7

Specimens examined: Dominican Republic: Boca Chica, 10 m, 4.XI.1972, Klapperich (Basel); Bani, 31.III.1973, Klapperich (Basel); Barahona, 6 km NW Fundacion, 1.IX.1983, W. E. Clark (AUBU); Peravia, 13 km NW Bani, 6.VIII.1979, C. W. O'Brien (CHAH).

Table 1. Checklist of species of Buprestidae recorded from Hispaniola. Literature citations are given only for those species described or reported since Fisher's (1925) monograph of Antillean Buprestidae.

Polycesta fisheri Obenberger, 1936:105
insulana Fisher, 1930:125
regularis Waterhouse?—type locality uncertain (Fisher 1925)
porcata (Fabricius)
Paratyndaris antillarum Fisher, 1939:156
Acmaeodera cruenta (Olivier)
Hilarotes nitidicollis (Laporte & Gory)
mannerheimi (Mannerheim)
Psiloptera aurata (Saunders)
aurata var. *domingoensis* Fisher, 1930:126
aurifer (Olivier)
Dicerca divaricata (Say)—introduced? (Fisher 1925)
Cinyra albonotata (Laporte & Gory)
Buprestis hispaniolae Fisher, 1939:157
striata Fabricius
maculativentris Say
Mixochlorus elegans Fisher
Peronaemis insulicola Fisher, 1939:159
Melanophila acuminata (Deg.)—Blackwelder 1944: 313
Tetragonoschema quadrata (Buquet)
Chrysobothris tranquebarica (Gmelin)
dentipes (Germar)
haitiensis Fisher, 1930:7
megacephala Laporte & Gory
chlorosticta Thomson
parvofoveata Fisher
hispaniolae Fisher
Actenodes bellula Mannerheim
embrik-strandi Obenberger, 1936:138
nobilis (Linnaeus)—Fisher 1930:127
Sambomorpha clarki, n. sp.—this study
Agrilus dominicanus Thomson
klapperichi n. sp.—this study
Taphrocerus hattiensis Fisher, 1949:348
Leiopleura darlingtoni Fisher, 1939:162
gibbipennis (Fisher), 1939:160
Neotrachys bilyi n. sp.—this study
Micrasta hispaniolae Fisher, 1939:166
monticola Fisher, 1939:165

Taphrocerus haitiensis Fisher, 1949:348

Specimens examined: Rep. Dominicana: Boca Chica, 10 m, 5.X.1970, 29.XI.1970, Klapperich (Basel); Bani, 65 m, 30.IV.1974, Klapperich (Basel); La Altag., 31 km N Higuey, 1.VIII.1979, G. B. Marshall (CHAH).

Leiopleura darlingtoni Fisher, 1939:162

Specimen examined: Dominican Republic: La Culata (La Vega), 1500 m, 18.III.1978, H. and A. Howden (CHAH).

Leiopleura gibbipennis (Fisher), 1939:160

Specimens examined: Dominican Republic: Boca Chica, 10 m, 5.X.1970, 29.XI.1970, Klapperich (Basel).

With the addition of the three species described above, the total fauna of Buprestidae reported from Hispaniola stands at 39, of which one is probably introduced and a second is questionable. Table 1 presents the list of species reported to date.

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FIRST NORTH AMERICAN RECORDS FOR *HARMONIA QUADRIPUNCTATA* (PONTOPIDDIAN) (COLEOPTERA: COCCINELLIDAE); A LADY BEETLE NATIVE TO THE PALAEARCTIC

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Abstract.—*Harmonia quadripunctata* (Pontopiddian), an Old World member of the tribe Coccinellini, is newly reported from three localities in the north eastern United States: Paterson and Westfield, New Jersey, and Mt. Kisco, New York. The North American specimens appear to have been derived from a single founding population which was established as early as 1924 and probably as the result of an adventive introduction. Key characteristics are given which will distinguish this species from the rest of the native and introduced North American Coccinellini. Habitat and prey preferences are briefly discussed.

Key Words: Coleoptera, Coccinellidae, *Harmonia*, aphidophagous, forest

Harmonia quadripunctata (Pontopiddian) is an Old World lady beetle of the tribe Coccinellini (*sensu* Sasaji 1971), which has become established in New Jersey and New York without any record of a deliberate introduction (Gordon 1985). A total of 8 specimens with North American collection localities have been recovered from 3 museums and one private collection. These specimens represent a minimum of 3 separate collection events (see map, Fig. 1) spanning a period of 54 and a half years and covering a linear distance of approximately 50 miles (=90 km). Although this is the first literature report on the occurrence of *H. quadripunctata* in North America, the unusually detailed specimen labels indicate that it has drawn the attention of earlier observers, some of whom were even apprised of its alien status. The diagnosis below will serve to distinguish the North American populations of *H. quadripunctata* from the rest of the introduced and native Coccinellini. Iablokoff-Khnzorian (1982) should be consulted for a synonymical bibliography.

Harmonia quadripunctata (Pontopiddian)
Fig. 1

Diagnosis of North American population: Form ovo-elliptic, weakly convex, 5.0 to 8.0 mm in length. Ground color of dorsal surfaces pale orangy brown; pronotum of fully maculate individuals with eleven punctiform black spots, one or two pairs sometimes faint or absent; elytron immaculate or with a pair of elongate black marks at lateral margin on each side of mid-line. Tibial spurs lacking. Postcoxal line of abdomen curved posterolaterally, closely approaching or joining posterior margin of segment; oblique dividing line present.

Harmonia quadripunctata will key to the genus *Mulsantina* Weise in Gordon (1985), however it can be readily distinguished from North American members of that genus by the larger body size and the presence of an

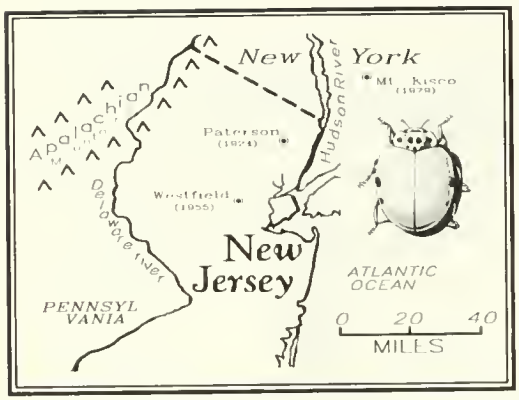

Fig. 1. Recorded North American collecting sites for *Harmonia quadripunctata* (ocellate dot); collection dates are given in parentheses. Habitus drawing of adult showing typical maculation of the North American population.

oblique dividing line in the postcoxal region of the abdomen. Although the genus *Harmonia* Mulsant is included in Gordon's key, the characters used are diagnostic only of the introduced species *H. dimidiata* (F.), which was the sole species known to occur in North America at the time. The distinctive dorsal color pattern of the North American population of *H. quadripunctata* is the best way to separate it from other members of its tribe. Members of the genus *Neoharmonia* Crotch, which also lack tibial spurs, possess fewer and larger pronotal maculae than *H. quadripunctata*.

Within its native range, *H. quadripunctata* exhibits extreme elytral color pattern polymorphism from nearly solid black, to various combinations and confluences of black spots against a pale background (Mader 1926–37, Iablokoff-Khnzorian 1982). Melanic individuals are rare in the southern part of the European continent, but a range of color forms can usually be found together at a given locality. This within population variation makes it impossible to speculate on the source area of the North American founding population even though they consistently fall at the extreme pale end of the color form spectrum.

I first became aware of the presence of *H. quadripunctata* in the United States when my colleague Stuart McKamey invited me to have a look at some coccinellids he had collected ten years earlier. I was disconcerted to find that the largest coccinellid in the box was completely unfamiliar to me, and could not be identified using any available keys to the North American fauna. The single specimen, which constitutes our most recent collection record of this exotic species, has a type-set label with the following data, "Mt. Kisco, NY Westchester Co. July 1979 Stuart McKamey Coll." and a neatly penned post script "only specimen collected, not very common."

I soon began to discover other North American specimens of *H. quadripunctata* which had previously escaped my notice. In the American Museum of Natural History, New York, a pair of the beetles were nestled inconspicuously in a unit tray of *Olla v-nigrum* Mulsant. The specimen labels contain the following data, "Westfield, N.J. Union Co., July 8, 1955 G.R. Ferguson [type-written, photographically reproduced?]/11192 C.A.F. '59 [hand-printed]." One of the specimens has two additional hand-printed labels sandwiched between the others. The white upper label reads "A very unusual immac. var 11192" and the lower blue label adds "I ought to swipe." These two specimens were collected twenty four years prior to the example captured by McKamey.

Some of the earliest collected specimens of North American *H. quadripunctata* were retrieved from the drawer of miscellaneous coccinellids in the Essig Museum, University of California, Berkeley. The find consists of a pair of card mounted beetles topping a stack of over-sized labels badly yellowed with age. The upper three labels bear the following information in a fine gray script "Paterson New Jersey Feb 27 1924 FM Schott/Bulaea lichatschovi Hummel/A Newcomer to United States found here by writer Native to Mediterranean region." A fourth label on a piece of torn and folded

paper appended to the bottom of the stack, offers the following correction in a robust black script "Harmonia quadripunctata Pontop. (North Europe)." The latter species identification has since been confirmed by comparing all of the U.S. specimens with a European series of *H. quadripunctata* from the U.S. National Museum of Natural History. Type specimens of *H. quadripunctata* have not been located (Gordon 1987b, Iablokoff-Khnzorian 1982), although workers seem to be in agreement on the identity of this common palaearctic species. The entomology collection of the California Academy of Sciences has three additional specimens of *H. quadripunctata* possibly derived from the series collected by Schott. These are labeled as follows: one specimen, "Paterson N.J. II.27.24 [no collector given]/ Nunenmacher collection" and two specimens on a single mount, "Bulaea lichchatchovi Paterson NJ Feb 27 [no year or collector given]/R. HOPPING COLLECTION." Someone had correctly filed these examples among the European *H. quadripunctata* but had either not published or simply failed to notice the unusual collection locality.

In addition to the eight specimens mentioned above, a search through the entomology collection of the Los Angeles County Museum revealed a single example of *H. quadripunctata* placed among the undetermined North American Coccinellidae. This individual showed the same distinctive color pattern as specimens collected in New York and New Jersey, but the glossy specimen label had faded to a uniform blue-gray. The source of the specimen must therefore be considered unsubstantiated.

Although ten years have passed since the last known collection of *H. quadripunctata* in North America, I am inclined to believe that it is still present. The three known collection dates, from earliest to most recent, were separated by intervals of about 30.5 and 24 years respectively during which no additional specimens were found. The recent ten year interval is therefore a comparatively short one, and since my search was by no means exhaustive, other specimens may well come to light. Several factors could have contributed to the low collection rate for this species as compared with others. In Europe, *H. quadripunctata* is most common in forested regions where fir, pine, poplar and chestnut grow (Iablokoff-Khnzorian 1982, Klausnitzer and Klausnitzer 1986). It is therefore less likely that the species would turn up in an agricultural setting, which is one of the places where coccinellid activities are most intensely monitored. In addition, the species is somewhat cryptically colored and its arboreal habits would further limit the chances of a casual sighting. The very reduced elytral markings of the North American populations of *H. quadripunctata* would also tend to make it resemble lightly marked individuals of other more common species, and it might be ignored by a collector who had already "filled his quota."

It would seem unlikely that the North American specimens of *H. quadripunctata* represent fortuitously intercepted individuals transported from Europe, or specimens collected in Europe which were subsequently mislabeled. The proximity of the three collection sites, and the remarkable similarity between the color patterns of the eight specimens, strongly suggests that they have descended from a single long established population. Probably the species was accidentally introduced to the east coast of North America on board European ships. This method of transport has been suggested for *Propylea quatuordecimpunctata* (L.) (Larochelle and Lariviere 1980) another European coccinellid which became established in the vicinity of Montreal. The habit of *H. quadripunctata* of forming large dormant aggregations in crevices of tree bark (Klausnitzer and Klausnitzer 1986, Bielawski 1961) would facilitate its successful transport in this manner.

Harmonia quadripunctata is one of four

exotic coccinelline species reported as established in eastern North America in the last couple of decades. The other three species are *Propylea quatuordecimpunctata* (Chantal 1972), *Coccinella septempunctata* L.(Angalet and Jacques 1975) and *Hippodamia variegata* (Goeze) (Gordon 1987a). In all four cases the established populations were first recorded near the east coast, from Montreal to New Jersey, and appear to have resulted from either undocumented or unintentional releases. The similarities which exist in the attributes of these four species are also interesting to note. They are all members of the tribe Coccinellini, are broadly endemic to the palaearctic, primarily aphidophagous, and form large aggregations during periods of dormancy. At this point the similarity ends. The three previously reported exotic species habituate herbs and grasses. Consequently these coccinellines have drawn considerable interest for their potential role as biological control agents of the introduced Russian wheat aphid *Diuraphis noxia* (Mordvilko). In contrast, *H. quadripunctata* is almost exclusively an arboreal species. Its habitat and prey preferences in the New World will most likely coincide with those of our native species of *Anatis* Mulsant and *Myzia* Mulsant. *Harmonia quadripunctata* will probably not play an important role in the suppression of aphids in most agricultural settings, with the possible exception of some orchard crops. European populations have been recorded on *aphis pomi* (Degeer) in apple orchards (Asgari 1966), but the species is most typically associated with *Cinara* sp. in forest and woodland habitats (Klausnitzer and Klausnitzer 1986).

Acknowledgments

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A NEW SPECIES OF WATER SCAVENGER BEETLE, *GUYANOBIUS SIMMONSORUM*, FROM BRAZIL (COLEOPTERA: HYDROPHILIDAE)

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Abstract.—A new species of water scavenger beetle, ***Guyanobius simmonsorum***, from a tributary of the Rio Xingú in the state of Pará, Brazil is described. The beetle is illustrated by pen and ink drawings and SEM micrographs and is distinguished from the only other species described in the genus, *Guyanobius adocetus* Spangler.

Key Words: Hydrophilidae, *Guyanobius simmonsorum*, new species, water scavenger beetle, Brazil

The genus *Guyanobius* was described for the single species, *G. adocetus* Spangler (1986) from Guyana. This second species of *Guyanobius* was collected in Brazil shortly after the description of the genus was published and is described to further define the genus. The specimens of this new species were collected from a small shaded tributary of the Rio Xingú where it flows through a lowland tropical rainforest in the Brazilian state of Pará. The specimens were collected during a biological survey of the area in advance of the construction of a hydroelectric dam on the river. If the dam is constructed as planned, the habitat from which this new species was collected will be inundated.

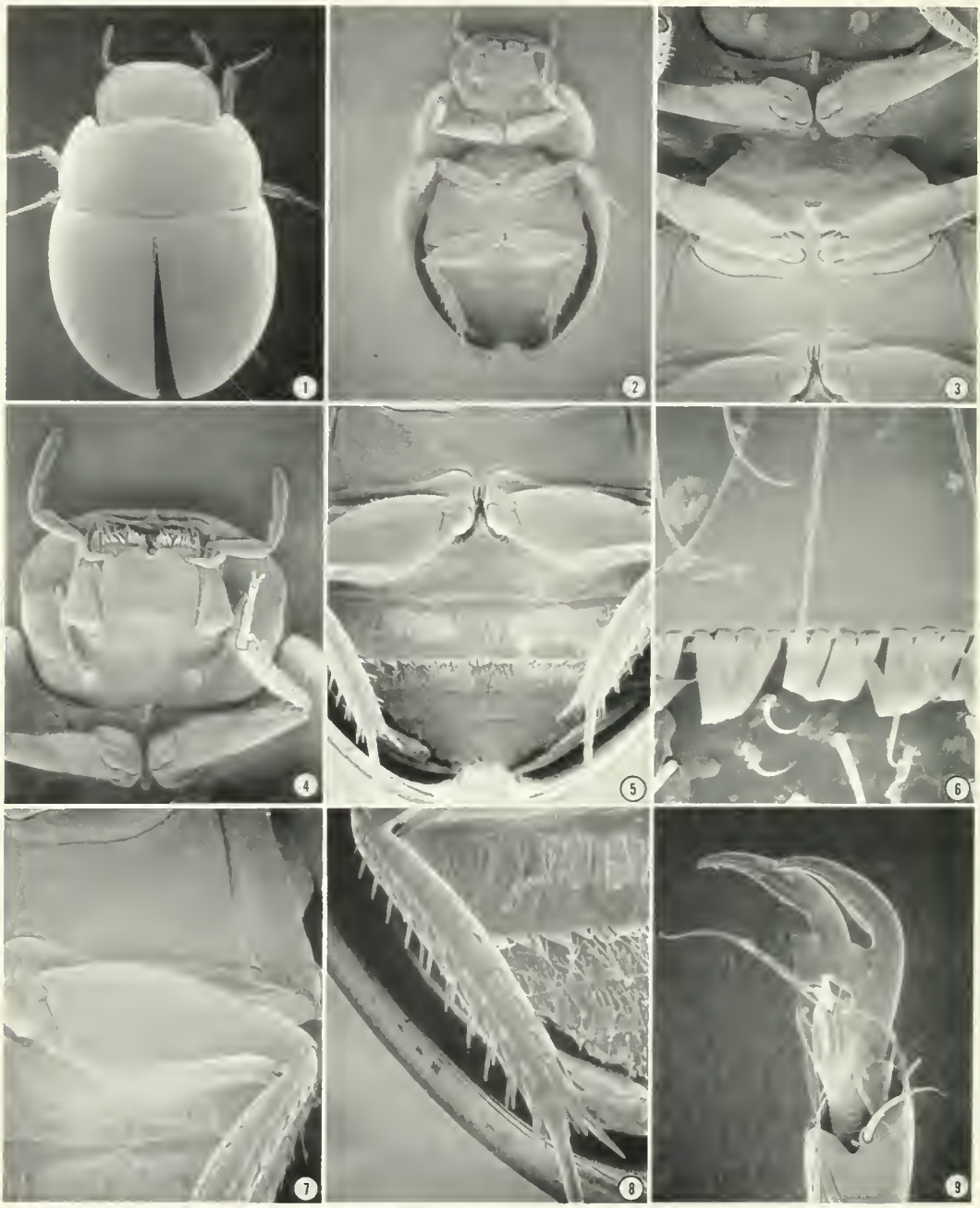
Guyanobius simmonsorum, NEW SPECIES
Figs. 1–11

Holotype ♂.—Form and size: Hemispherical, strongly convex dorsally (Figs. 1, 2). Length, 2.98 mm; greatest width, 2.24 mm.

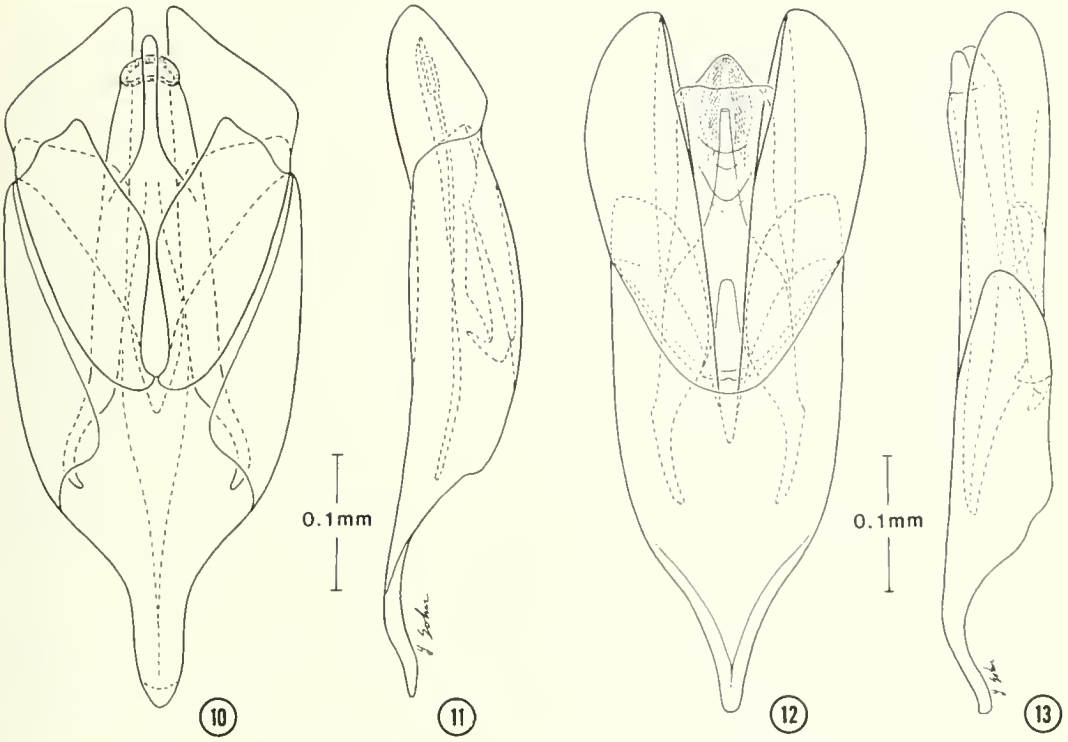
Color: Shiny black dorsally except narrow band on anterior margin of head, lateral margins of pronotum, and very narrow lateral margins and posterior half of sutural margins of elytra dark reddish brown. Venter light reddish brown except metasternal disc and middle of abdominal segments 1 and 2 slightly darker reddish brown.

Head: Very finely, sparsely punctate; discal punctures separated by 4 to 8 times puncture diameter; punctures across base of head between eyes smaller and sparser than discal punctures and separated by 3 to 4 times puncture diameter. Clypeus (Fig. 4) strongly, broadly expanded anteriorly and laterally, concealing labrum (Fig. 4); lateral margin extending deeply into eye; anterior margin feebly arcuate apicomedially. Mentum shallowly concave, moderately broad and moderately emarginate apicomedially; surface moderately coarsely, densely punctate; punctures separated by 3 to 5 times puncture diameter. Submentum shallowly concave and densely, finely punctate; each puncture bearing a seta.

Thorax: Pronotum widest at posterior third; strongly rounded laterally; shallowly emarginate apically and feebly arcuate apicomedially (Fig. 1); truncate posteriorly; narrowly rimmed laterally and anterolaterally behind eyes; not rimmed posteriorly except at posterolateral angles; sides nearly



Figs. 1–9. *Guyanobius simmonsorum,* new species, ♂: 1, habitus, dorsal view, ×30; 2, habitus, ventral view, ×25; 3, prosternum, mesosternum, metasternum, ×60; 4, head, ventral view, ×60; 5, metasternum and abdomen, ×60; 6, setation, hind margin of abdominal sternum 2, ×1000; 7, hind femur, ×100; 8, hind tibia, ×120; 9, protarsal claws, ×800.



Figs. 10–13. 10, 11. *Guyanobius simmonsorum*, new species, genitalia, ♂: 10, ventral view; 11, lateral view. Figs. 12, 13. *Guyanobius adocetus* Spangler, genitalia, ♂: 12, ventral view; 13, lateral view.

vertical, extending well below prosternum; discal punctures finer and slightly more widely separated than discal punctures of head; most punctures separated by 6 to 8 times puncture diameter; lateral punctures slightly coarser. Prosternum with distinct, keel-like, medial process on anterior third; keel extending beyond anterior margin of prosternum; a tuberculate process on posteromedial margin (Figs. 2–4). Mesosternum with moderately broad, triangular protuberance between and slightly in front of mesocoxae (Fig. 3). Metasternum shiny, glabrous (except a few setae behind mesocoxae); with raised, broadly triangular area medially; sides shallowly concave; metepisterna pubescent. Procoxae sparsely finely setose laterally but with 12 very stout, darker setae ventroapically. Profemora densely punctate and pubescent ventrally on basal two-thirds; mesofemora and metafemora, except apical fourth, densely punctate and pubescent ventrally (Fig. 7); male protarsal claws with broad, tooth-like base (Fig. 9); metatarsal claws without tooth-like base. Elytra with sides nearly vertical, extending well below mesosternum, metasternum, and abdominal sterna (Fig. 2); without sutural striae; finely, sparsely punctate; punctures larger than those on pronotal disc and disarrayed except as follows. Each elytron with 1 incomplete, indistinct row of moderately coarse, shallow punctures laterally, punctures separated by about 2 times puncture diameter; lateral punctate row starting a short distance behind humeral area and extending a distance about equal to ⅕ length of elytron; with 4 additional poorly defined rows of widely separated, seta-bearing punctures. Lateral margin of each elytron narrowly rimmed from base to apex. Scutellum flat, triangular; surface finely, sparse-

ly punctate; punctures separated by 3 to 9 times puncture diameter.

Abdomen: Sterna 1 and 2 strongly concave; with coarse, sparse, seta-bearing punctures; punctures separated by 2 to 4 times puncture diameter; posterior margin of sternum 2 with a dense row of robust setae (Figs. 5, 6). Remaining sterna finely and densely punctate and densely pubescent.

Male genitalia: As illustrated (Figs. 10, 11).

Female.—Similar to male except average size is larger.

Variations.—Males (N = 10) varied in length from 2.86 to 3.30 mm (=3.05) and in width from 2.07 to 2.39 mm (=2.23); females (N=10) varied in length from 2.94 to 3.53 mm (=3.27) and in width from 2.30 to 2.60 mm (=2.47). The concavity of sterna 1 and 2 of some specimens bears a lens-shaped hyaline mass as is seen on specimens of *Laccobius* and *Chaetarthria*. The hyaline mass is not present on many specimens because it is easily dislodged when specimens are placed in alcohol.

Comparative notes.—*Guyanobius simmonsorum* is very similar to *G. adocetus* Spangler (1986) from Guyana but may be distinguished from it as follows (character state for *G. simmonsorum* stated first). Elytral rim present from base to apex vs rim disappearing at apical fourth; elytron with 1 incomplete, indistinct row of moderately coarse shallow punctures laterally and behind humeral area vs elytron with 3 rows of coarse, distinct punctures laterally behind humeral area. Mentum with entire surface coarsely, densely punctate vs surface of mentum moderately coarsely, sparsely punctate laterally and meson almost glabrous. Parameres (Figs. 10, 11) with apices subtriangular vs apices of parameres rounded (Figs. 12, 13).

Type data.—*Holotype male:* BRAZIL: PARA: Altamira (ca. 60 km S), Rio Xingú Camp, 52°22′W, 3°39′S, 14 Oct 1986, P. J. Spangler & O. S. Flint, colln #23, left branch off 1st jungle stream on trail 1; deposited in the Museu de Zoologia, Universidad de Sao Paulo, Brazil. Allotype: same data as holotype.

Paratypes: Same data as holotype, 24 ♂, 18 ♀; same data except: 3 Oct 1986, colln #6, 11 ♂, 11 ♀; 7 Oct 1986, colln #12, 3 ♂, 2 ♀.

Paratypes will be deposited in the British Museum (Natural History), London; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Institut Royal de Histoire Naturelle de Belgique, Bruxelles; Museo Argentina de Ciencias Naturales, Buenos Aires; Museo de Zoologia, Universidad de Sao Paulo, Sao Paulo; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Zoologische Staatssammlung München, München.

Etymology.—The specific epithet *simmonsorum* is named for the Jerry L. Simmons family for their interest in and support of aquatic Coleoptera research at the Smithsonian Institution.

Habitat.—The type material was collected from a small, shaded stream that flowed slowly from pool to pool through the jungle near the base camp. The stream was at an altitude of 90 meters; had a velocity of 2 m/min; was clear, a meter wide, and up to 75 cm deep; had a sand and leafy substratum, and colorimetric readings of hardness, 0, and a pH 5. The water temperature was 25.5°C and the air temperature was 27.5°C at the time the specimens were collected.

The following aquatic insects were associated with *G. simmonsorum* in the same habitat: COLEOPTERA: DRYOPIDAE: *Pelonomus, Dryops.* DYTISCIDAE: *Laccophilus, Derovatellus, Desmopachria,* Bidessines. ELMIDAE: *Tyletelmis, Heterelmis*; HYDRAENIDAE: *Hydraena*; HYDROPHILIDAE: *Derallus, Paracymus, Helochares, Hydrochus, Phaenonotum, Notionotus*; LUTROCHIDAE: *Lutrochus.* GYRINIDAE: *Gyretes.*

HETEROPTERA: BELOSTOMATIDAE: *Belostoma.* GERRIDAE. HELOTRE-

PHIDAE: *Helotrephes*. HYDROMETRIDAE: *Hydrometra*. NAUCORIDAE: *Ambrysus*. NEPIDAE: *Ranatra*. VELIIDAE: *Microvelia, Paravelia, Rhagovelia*.

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MORPHOLOGY AND MATING CONFIGURATION OF GENITALIA OF THE ORIENTAL COCKROACH, *BLATTA ORIENTALIS* L. (BLATTODEA: BLATTIDAE)

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Abstract.—Male and female genitalia of the oriental cockroach, *Blatta orientalis* L., are redescribed and illustrated. New terms are assigned to lobes of the left and right phallomeres of the male genitalia. Aspects of the mating behavior are presented, including the function of the titillator in initiating copulation. The configurational arrangement of the genitalia during copulation is described and illustrated, including the functions and positions of the three phallomeres of the male genitalia with the valvulae of the female ovipositor. The five modified lobes of the male left phallomere and the scoop-like ventral phallomere function mainly to stabilize the female valvulae on each side, while the serrata of the right phallomere performs to separate the paired first valvulae from the center. This spreading configuration provides for the successful transfer of spermatophore.

Key Words: *Blatta orientalis*, morphology, genitalia, copulation

The oriental cockroach, *Blatta orientalis* L., is native to North Africa and now is distributed throughout the temperate regions of the world (Cornwell 1968, Cochran 1982, Woo 1987). It is the dominant cockroach pest species in Great Britain (Ragge 1965, Cornwell 1968). Mampe (1972) and Piper and Frankie (1978) reported it to be a seasonal household pest in portions of the northwestern, midwestern, and southern United States. The pest status of the oriental cockroach has been documented by Thoms and Robinson (1986, 1987).

Snodgrass (1933) provided a comprehensive description of the female genitalia and related musculature of *B. orientalis*. Snodgrass (1937) also described and illustrated the male genitalia of this species and presented a hypothetical plan for the phylogenetic development of the male genitalia and corresponding phallic musculature. Marks and Lawson (1962) and McKittrick (1964) compared and illustrated ovipositors of several cockroach species. They considered the structure of the ovipositor of the oriental cockroach very similar to that of *Periplaneta americana* (L.) and other *Periplaneta* species. The morphology of the genitalia of *B. orientalis* has not been re-examined since the early descriptions and interpretations by Snodgrass (1933, 1937) and McKittrick (1964). This study provides an overall revision of the female and male genitalia and describes the mating behavior of the oriental cockroach. The configurational arrangement of the genital structure during copulation are also described and illustrated.

MATERIALS AND METHODS

Adult cockroaches were obtained from field and laboratory colonies. Genitalia of

male and female adults were examined and illustrated using an optical dissecting microscope and ocular grid. Specimens were preserved in 70% ethanol and treated with 10% aqueous potassium hydroxide (KOH) for about 24 hours at room temperature before examination and illustration. The genitalia were preserved in 70% ethanol with a few drops of glycerine for further examination and photography.

The terms and abbreviations used in this study to describe the male and female genitalia of *B. orientalis* were adopted from those used by Snodgrass (1933, 1937) and McKittrick (1964). New terms were assigned to some structures of the male genitalia.

For the study of the configurational arrangement of genitalia during copulation, male and female adults were separated soon after the final molt and kept segregated for 7 days. Mating behavior was observed and recorded when the male and female were placed together. After coupled for 20–30 minutes, the male and female were anesthetized with carbon dioxide, then killed with ethyl acetate. The configuration of the male and female genitalia during copulation was determined by dissecting the genital segments of 23 pairs of freshly killed specimens or those preserved in 10% KOH for 24 hours.

Results and Discussion

Female genitalia.—The reduced eighth and ninth abdominal segments, or the genital segments, bear appendages that form the ovipositor of the female. The seventh abdominal sternum (SVII) is expanded and prolonged posteriorly to form two large, valve-like lobes (SVIIL) that conceal the ovipositor. Dorsal to the SVIIL, the paired clefts are the tenth tergum (TX). The cerci lie beneath the basal corners of the tenth tergum. Beneath the TX at the posterior end of the abdomen are a pair of sclerotized paraprocts (PAPT). These may be remnants of the eleventh abdominal segment. The

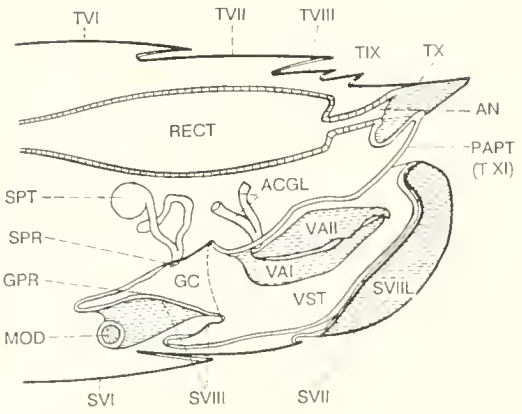

Fig. 1. Diagrammatic median view of female *Blatta orientalis* genital segment. ACGL, accessory gland; AN, anus; GC, genital chamber; GPR, gonopore; MOD, median oviduct; PAPT, paraproct (T XI); RECT, rectum; SPR, spermathecal pore; SPT, spermatheca; SVI, sixth sternum; SVII, seventh sternum; SVIII, eighth sternum; SVIIL, lobe of seventh sternum; TVI, sixth tergum; TVII, seventh tergum; TVIII, eighth tergum; TIX, ninth tergum; TX, tenth tergum; VAI, first valvula; VAII, second valvula; VST, vestibulum. (Modified after Snodgrass 1933).

anus lies centrally in the membrane between the pair of paraprocts and the tenth tergum (Fig. 1).

There are two internal chambers, the vestibulum (VST) and the genital chamber (GC), which are formed by the modified SVII, SVIII, SIX, SX, and TIX. The ovipositor lies in the vestibulum, with the seventh sternum as the floor of the chamber. Anterior to vestibulum is the smaller genital chamber, with the invaginated eighth sternum as its floor. The median oviduct (MOD) empties into the floor of the genital chamber by way of the gonopore (GPR). The spermatheca (SPT) possesses a pore which empties into the roof of the genital chamber. The accessory glands (ACGL) open on the roof of the vestibulum between the second pair of valvifers (VLFII) near their bases (Figs. 1, 2).

The roof of the genital chamber possesses a pair of large, lateral sclerites or basivalvulae (BSV) and a median sclerite, or spermathecal plate (SPPL) (Fig. 2). These

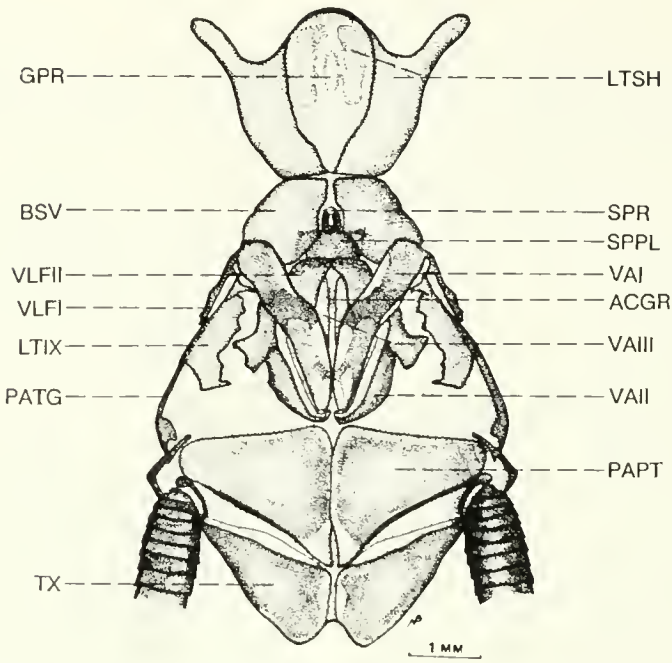

Fig. 2. Female genitalia of *B. orientalis* (ventral view). ACGR, acessory gland pore; BSV, basivalvula (SVIII); GPR, gonopore; LTIX, ninth laterosternite (SIX); LTSH, laterosternal shelf (SVIII); PAPT, paraproct (T XI); PATG, paratergite (TIX); SPR, spermathecal pore; SPPL, spermathecal plate; TX, tenth tergum; VAI, first valvula; VAII, second valvula; VAIII, third valvula; VLFI, first valvifer; VLFII, second valvifer.

sclerites may represent the secondary sclerotizations between the eighth and ninth segments. The floor of the genital chamber possesses two pairs of sclerites, or the laterosternal shelves (LTSH), which are derived from the eighth sternum. The gonopore lies in the membrane between the laterosternal shelves.

The roof of the vestibulum, consisting of the fused sterna of the ninth and tenth abdominal segments, supports the base of the ovipositor. The slender sclerite, or paratergite (PATG), on the roof edge of the vestibulum is derived from the ninth tergum. The irregular sclerites, the ninth laterosternites (LTIX), on the roof of the vestibulum, with the anterior ends fused to the first valvifers (VLFI), are the sternites of the ninth segment.

The ovipositor has two pairs of valvifers and three pairs of valvulae. The sclerotized first pair of valvulae (VAI) of the ovipositor are widely divergent at their bases, fused to the first pair of valvifers which may be derived from the eighth segment. The sclerotized second pair of valvulae (VAII) arise laterally from the fused, highly sclerotized second pair of valvifers. The pair of third valvulae (VAIII) are largely membranous and arise from the second valvifers, mesad of the second valvulae and beneath the first valvulae (Fig. 2).

Male genitalia.—The ninth abdominal segment, or the genital segment, bears appendages that form the genitalia of the male (Fig. 3). The bilobed tenth tergum (TX) forms the roof of the male genital chamber. The ninth sternum (SIX) bears a pair of small styli (STY), which may represent the remnants of the male gonopods. The paired paraprocts (PAPT) lie beneath the tenth tergal plate. The anus is situated in the membrane between the tenth tergum and the paraprocts.

The external genitalia of the male consist of genital lobes or phallomeres (PHM) as-

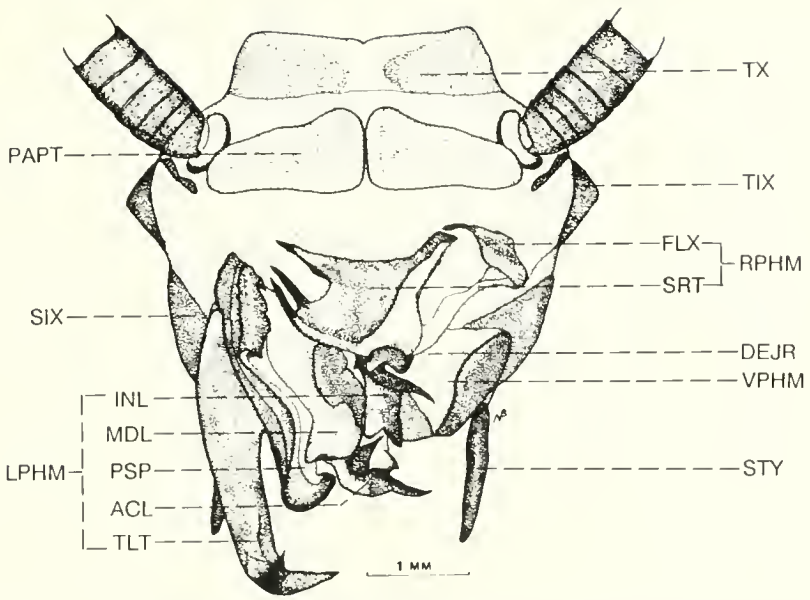

Fig. 3. Male genitalia of *B. orientalis* (dorsal view). ACL, acutolobus; DEJR, ejaculatory duct pore; FLX, falax; INL, inner lobe; LPHM, left phallomere; MDL, middle lobe; PAPT, paraproct; PSP, pseudopenis; RPHM, right phallomere; SIX, ninth sternum; SRT, serrata; STY, stylus; TIX, ninth tergum; TLT, titillator; TX, tenth tergum; VPHM, ventral phallomere.

sociated with the genital pore. Phallomeres consist of three major parts: the left, right, and ventral phallomere.

The right phallomere (RPHM) has two sclerites, the serrata (SRT) and falax (FLX), which lie on the center of the genital chamber towards the right. The serrata of the right phallomere, which lies in the center of the genital chamber, bears a fork-like sclerotized structure with two sharp processes on the left and a highly sclerotized hook-like structure on the posterior right. Snodgrass (1937) considered the serrata to be composed of three sclerites. The "right lobule" is membranous in nature. Since there are no sutures and sulci present in the serrata, there is no evidence to divide the serrata into three sclerites. The only difference is the unequal degrees of sclerotization in different portions of the serrata. The falax of the right phallomere is a simple sclerite situated laterally and joined with the right side of the serrata.

The left phallomere (LPHM) is the most complicated phallic organ of the male genitalia. It bears five elongated structures: the titillator (TLT), the outermost elongated and sclerotized lobe with a hook at the base of its pointed tip; the pseudopenis (PSP), mesad of the titillator with a bulbous tip; the middle lobe (MDL), next to the inner side of pseudopenis and partially sclerotized; the acutolobus (ACL), beneath the middle lobe, with a sclerotized hook and a partially sclerotized tooth-like process on its inner side; and the inner lobe (INL), the small innermost lobe with a sclerotized process on its posterior right end.

The ventral phallomere (VPHM) is a broad, scoop-like lobe projecting to the right from the posterior surface of the genital membrane. The ejaculatory duct (DEJ) empties into the floor of the genital chamber by way of the male gonopore, which is situated on a small membranous elevation on the base of the ventral phallomere.

Mating behavior and configurational arrangement of genitalia at copulation.—The mating behavior of *B. orientalis* observed in this study was very similar to previous

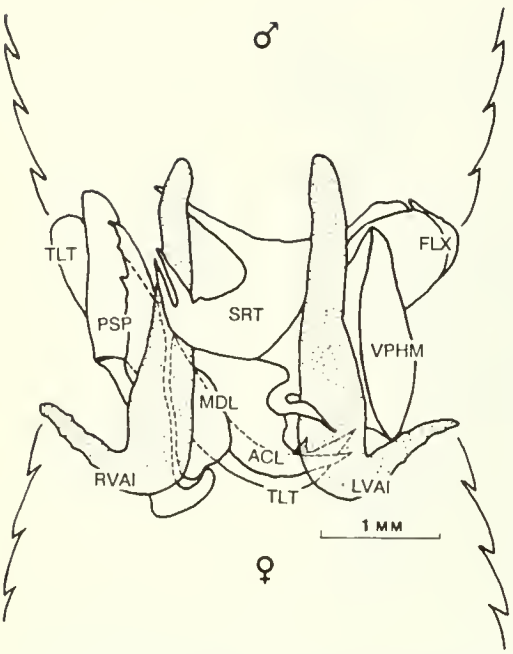

Fig. 4. Configurational arrangement of genitalia during copulation (dorsal view). ACL, acutolobus; FLX, falax; LVAI, first left valvula; MDL, middle lobe; PSP, pseudopenis; RVAI, first right valvula; SRT, serrata; TLT, titillator; VPHM, ventral phallomere.

reports by Roth and Willis (1952) and Barth (1970). The description by Barth (1970) is more similar to the observations in this study. A male is usually stimulated by contact with a female body or antennae. The aroused male typically raises his wings, and extends his abdomen, and depresses it against the substratum. Simultaneously, the titillator of the left phallomere is rhythmically protruded out of the genital chamber. The male actively searches for females and frequently attempts to back under a female from in front of her. A receptive female will move forward on the male, with her mouthparts continuously contacting his abdominal terga at the same time the male moves backwards. When the female moves to "feed" on the first abdominal tergum of the male, she spreads apart her vestibulum. Simultaneously, the male extends his abdomen and rapidly raises and inserts his genital segments to the vestibulum of the female. The hooked titillator of the left phallomere is the first phallic organ which fastens to the ovipositor to achieve the connection. Once the connection is established, the male swings out from underneath the female and rotates 180° to attain an opposed position. Then, the distal segments of both the sexes are tightly hooked together by way of the male genital organs inserted in the vestibulum between the ovipositor and the lobes of SVII. Copulation was observed to last 30 to 45 minutes.

During copulation the titillator and acutolobus of the left phallomere spread a great distance from the original left-side position towards the right and assist the ventral phallomere to clasp the first left-valvula (LVAI) of the ovipositor (Fig. 4). Both structures have strong, pointed tips and hooks, which help to clasp the valvulae tightly. The other lobes i.e. the inner lobe, middle lobe, and pseudopenis of the left phallomere hold the first right-valvula (RVAI) on the left-ventral side. The pseudopenis has a groove on its inner side, in which the first right-valvula is placed. The ventral phallomere grips the first left-valvula on its groove, which is formed by means of folding its distal perimeter upwards. The forks of the serrata grip the first right-valvula from the inner side towards outside, which hold the valvula along with the three lobes of the left phallomere. The hook of the serrata grips the first left-valvula from the inner side towards the outside. It is associated with the ventral phallomere, the titillator, and acutolobus. The serrata of the right phallomere keeps the first pair of valvulae open from the center, so that the other two pairs of valvulae and the genital chamber are exposed. The male gonopore, with associated membrane on the base of the ventral phallomere, projects into the female genital chamber where the spermathecal sac and the female gonopore are located. This spreading of the valvulae provides for the successful transfer of

a spermatophore from the male ejaculatory duct onto the ventrally projecting spermathecal papilla of the female. Gupta (1947) reported a similar mating behavior and configurational arrangement of genitalia at copulation for *P. americana*. He illustrated the coupled structure of the male and female genitalia and pointed out that the titillator of the male genitalia was important in forcing open the female vestibulum (gynatrium) to allow the entry of the male genitalia. He also described the importance of the right phallomere which functioned as the main clasping organ to hold the valvulae of the female genitalia during copulation. The configurational arrangement of the genitalia of *B. orientalis* is similar to that of *P. americana* during copulation.

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A NEW *DARJILINGIA* (SYMPHYTA: TENTHREDINIDAE) FROM TAIWAN

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Abstract.—***Darjilingia varia*** sp. nov. from Taiwan is described and illustrated.

Key Words: *Darjilingia*, Tenthredinidae

The genus *Darjilingia* was known only by its type species, *D. gribodoi* (Konow), from India (Himalayas) and Burma. It probably does not occur in Borneo as Konow stated (Konow 1896; Malaise 1934). Malaise (1963) questionably recorded the genus from Formosa. Through the courtesy of Dr. A. Shinohara, Department of Zoology, National Science Museum (Nat. Hist.), Tokyo, I had an opportunity to examine four specimens of *Darjilingia* that he collected in Taiwan in 1976 and 1977. These specimens represent a new species, and I describe the species below. They are the first definite record of *Darjilingia* from Taiwan.

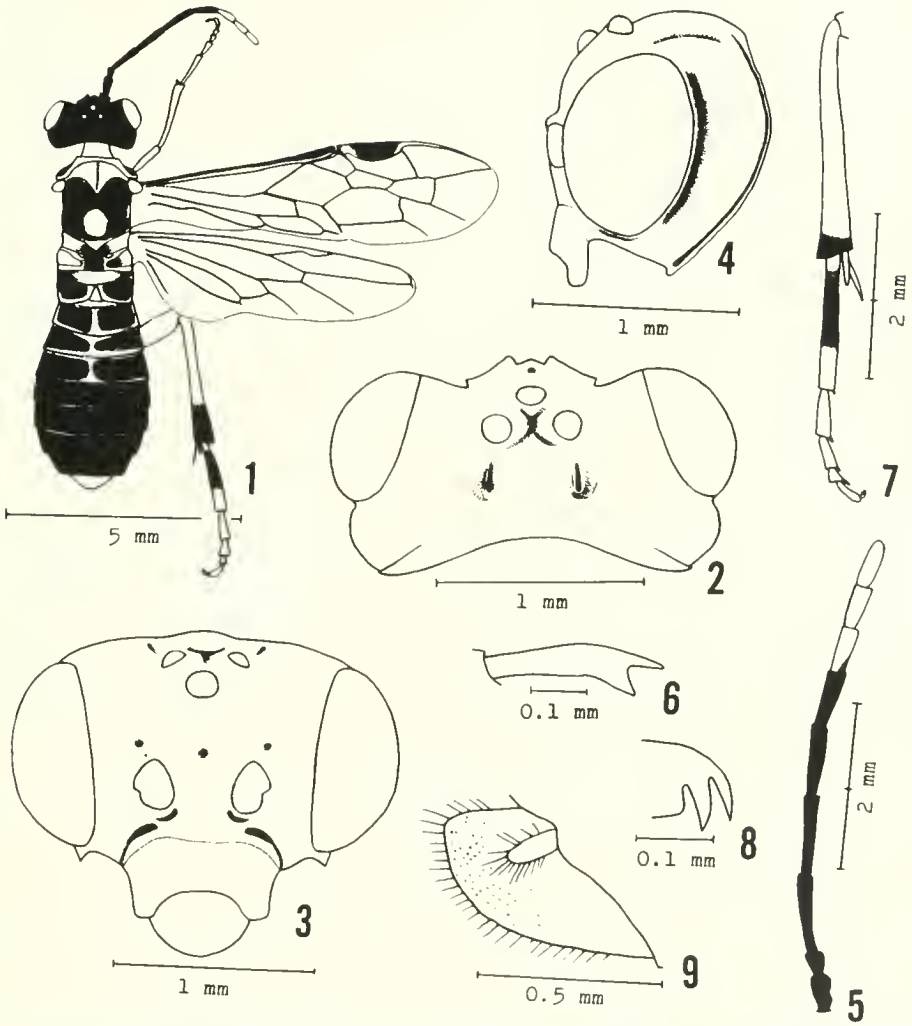
Darjilingia varia Togashi, NEW SPECIES
(Figs. 1–18)

Female.—Length 8.5 mm. Head and thorax black, with following parts yellowish white: clypeus, labrum, mandible except for apex, maxillary and labial palpi, posterior margin of pronotum, oval macula on mesoscutellum, cenchri, metascutellum, a small spot on upper portion and an elongate macula on lower portion of mesopleuron (Fig. 15), and posterior portion of meseepimeron. Apex of mandible red. Parapteron, tegula, and a small spot on central portion of mesonotal lateral lobes (Fig. 12) reddish yellow. Wings hyaline, stigma except for basal portion and veins dark brown. Basal portion of stigma of forewing whitish (Fig. 1). Legs reddish brown but all coxae, trochanters, and basal ⅓ of hind femur yellowish white; knee of hind femur, apical portion of hind tibia, and hind basitarsus except for apical ⅓ black; apical ⅓ of hind basitarsus and following four segments of hind tarsus yellowish white (Fig. 7). Abdomen reddish brown but 1st tergite and 5th to 8th tergites dark brown or with large dark brown maculae (Fig. 1); 9th tergite yellowish white; 8th sternite, 2nd valvifer, and sawsheath dark brown to black.

Head seen from above transverse; postocellar area slightly convex; lateral furrows distinct and deep; postocellar and interocellar furrows slightly depressed (Fig. 2); OOL: POL:OCL = 1.7:1.0:2.4; lateral and median foveae slightly depressed; ratio between antenno-ocular distance and distance between antennal sockets about 0.7:1.0; apical margin of clypeus as in Fig. 3; occipital carina distinct but upper portion nearly obsolete (Figs. 2, 4); post-orbital groove distinct (Fig. 4); malar space narrow, nearly ½ as long as diameter of front ocellus.

Antenna (Fig. 5) nearly as long as costa of forewing; relative lengths of segments about 1.6:1.0:3.6:3.5:3.2:2.5:2.0:1.8:2.2.

Thorax: normal; mesoscutellum slightly raised. Wing venation as in Fig. 1; anal cell of hindwing sessile. Legs: front inner tibial



Figs. 1–9. *Darjilingia varia* Togashi sp. nov. 1, dorsal view (paratype); 2, head, dorsal view; 3, head, front view; 4, head, profile; 5, antenna, lateral view; 6, front inner tibial spur, lateral view; 7, hind tibia and tarsus, lateral view; 8, tarsal claw; 9, sawsheath, lateral view.

spur as in Fig. 6; tarsal claw with a large inner tooth, and with distinct basal lobe (Fig. 8); hind basitarsus slightly longer than following four segments combined (ratio between them about 1.00:1.07).

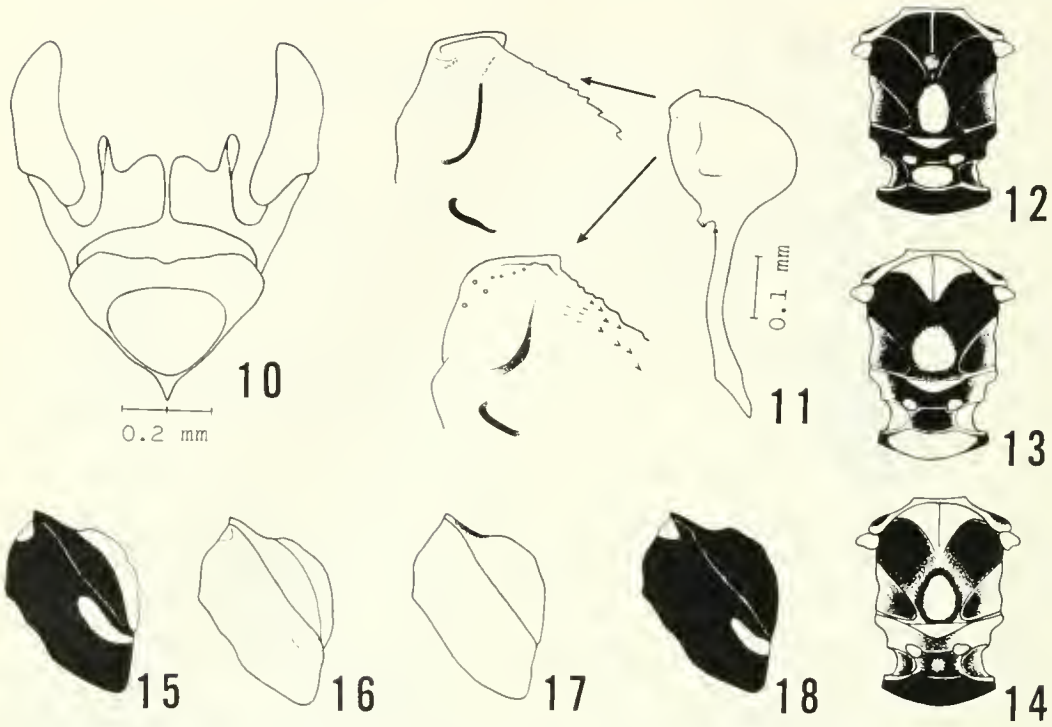
Abdomen: sawsheath as in Fig. 9.

Punctuation.—Head and thorax nearly impunctate, shining; abdominal tergites nearly impunctate, shining.

Male.—Length 7.5 mm. Coloration as in female but 2nd to 6th tergites reddish brown, and last two abdominal segments yellowish white. Structures as in female except for sexual segments. Male genitalia and penis valve as in Figs. 10 and 11.

Holotype: female, 13. III. 1977, Wushe, Taiwan.

Paratypes: 1 female, 4. V. 1976, Meifeng-Sungkang, Taiwan; 1 male, 3. V. 1978, Nanshanchi, Taiwan; 1 female, 13. III. 1979, Wulai, Taiwan. Holotype and two paratypes (female and male) are deposited in the



Figs. 10–13. Figs. 10–11. Male genitalia and penis valve of *D. varia* sp. nov. 10, male genitalia; 11, penis valve. Figs. 12–14. Colour pattern of thorax of *D. varia* sp. nov. 12, typical form (holotype); 13 and 14, variations (paratypes). Figs. 15–18. Colour pattern of mesopleuron of *D. varia* sp. nov. 15, typical form (holotype); 16 and 17, variations (female paratypes); 18, typical form (male paratype).

Department of Zoology, National Science Museum (Nat. Hist.), Tokyo. One paratype is deposited in the U.S. National Museum, Washington, D.C.

Variation.—The coloration of the praescutum is reddish brown in the paratypes (Figs. 13, 14). The coloration of the metascutellum varies from black (Fig. 13) to yellowish white (Fig. 12), and the coloration of the mesopleuron varies from black (Fig. 15) to pale reddish yellow (Fig. 17). Also, the coloration of the abdomen is dark to light reddish yellow.

Remarks.—This new species closely resembles *D. gribodoi* (Konow 1896) from Borneo (?), Burma, and India (Darjeeling, Khasia Hills, and Assam), but it is easily distinguished from *gribodoi* by the coloration of the basal three segments of the antenna (in *gribodoi,* the basal three segments of the antenna are reddish yellow to reddish brown), by the coloration of the apical portion of the hind tibia and hind basitarsus (in *gribodoi,* the legs are reddish yellow except for the basal portion of the coxae, and the hind basitarsus is black), and by the length of the antenna (in *gribodoi,* the antenna is nearly as long as the body length).

Acknowledgments

I wish to express my sincere thanks to Dr. A. Shinohara, Department of Zoology, National Science Museum (Nat. Hist.), Tokyo, for the loan of the valuable specimens and to Dr. David R. Smith, Systematic Entomology Laboratory, USDA, Washington, D. C., for reviewing the manuscript.

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HOST SPECIFICITY OF *CHAETORELLIA AUSTRALIS* (DIPTERA: TEPHRITIDAE) FOR BIOLOGICAL CONTROL OF YELLOW STARTHISTLE (*CENTAUREA SOLSTITIALIS*, ASTERACEAE)

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Abstract.—The flower head tephritid fly *Chaetorellia australis* Hering was studied to determine its host specificity for biological control of *Centaurea solstitialis* L. (yellow starthistle) in the United States. Flies from flower heads of *C. cyanus* L. collected in northern Greece were tested for oviposition and development on nine plant species in no-choice host tests during the summers of 1986–87 in Albany, California. Oviposition and development occurred on only two species: flies damaged 93.7% (1986) and 79.6% (1987) of the heads of *C. solstitialis* and 85.8% of the heads of *C. cyanus*. No evidence of oviposition and development occurred on the other test plant species: *Centaurea americana* Nutt., *Centaurea rothrockii* Greenm., *Carthamus tinctorius* L., *Cirsium occidentale* (Nutt.) Jeps., *Helianthus annuus* L., *Zinnia elegans* Jacq., and *Lactuca sativa* L.. More than 92% of the pupal fly-yielding flower heads produced only one pupal fly, while less than 8% of these flower heads had two pupal flies, indicating that the fly is not particularly gregarious.

Key Words: biological control, weed, rangeland, insect

Yellow starthistle (*Centaurea solstitialis* L., Asteraceae) is a winter annual that is a naturalized weed primarily in the western United States. Surveys indicate that it occurs in 208 counties in 23 states within the U.S. (Maddox et al. 1985), and infestations in California alone have reached an estimated 3.25 million gross hectares (Maddox and Mayfield 1985). The weed is a pioneering species that is especially invasive on disturbed lands. Its primary economic impact is on rangelands where it reduces livestock productivity because of its unpalatability, competitiveness, and toxicity to horses (Maddox et al. 1985). Yellow starthistle is believed to be native to the eastern Mediterranean Basin and western Asia (Prodan 1930). Multiple introductions have probably occurred in the U.S. (Maddox and Mayfield 1985). An analysis of seeds contained in adobe bricks from early buildings in California indicates that yellow starthistle was introduced in the nineteenth century after 1824 (Hendry 1931, Hendry and Bellue 1936, Maddox and Mayfield 1985).

A search for natural enemies of yellow

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starthistle and other weedy members of the thistle tribe (Cardueae) was begun in Europe in the late 1950's (Zwolfer et al. 1971). In 1985 the flower head weevil, *Bangasternus orientalis* (Capiomont) (Coleoptera: Curculionidae), was introduced from northern Greece for biological control of yellow starthistle and is now successfully established in several western states (Maddox et al. 1986). Sobhian and Zwolfer (1985), in their studies of the yellow starthistle flower head–insect host system, show that the larvae of about 20 phytophagous insect species utilize the flower heads of yellow starthistle in the Mediterranean Basin and regions in the northern half of the Balkan Peninsula. *Chaetorellia australis* Hering is one of those flower head insects that offers promise as a biological control agent. Tephritid fly species, including *C. australis*, are considered to be one of the most important elements within the guild of insects utilizing the flower heads (Sobhian and Zwolfer 1985). They are important flower head feeders on asteraceous species in general, and are often either strongly monophagous or stenophagous on their host plants. Flower head feeders may be especially important as biological control agents because yellow starthistle is an annual weed that relies solely on seed production to reproduce. This fly has previously been referred to as *Chaetorellia hexachaeta australis* Hering (White and Marquardt 1989).

Biology

The biology of *C. australis* in northern Greece is as follows (Sobhian and Zwolfer 1985, Sobhian and Pittara 1988): Three generations of flies occur per year. Females begin oviposition after adult emergence in the spring. Under uncrowded conditions, a female usually oviposits beneath an involucral bract one egg per host flower head. Oviposition occurs preferentially on mature, closed flower head buds. Each egg characteristically possesses a long filament, which can extend beyond the margins of a bract. Under laboratory conditions, females may oviposit up to 243 eggs during an ovipositional period of up to 60 days. Hatched larvae tunnel through the involucre into the interior of the flower head, where they tunnel through and feed on many ovaries and developing achenes. In one limited test, a single larva destroyed an average of 86.3% of the seeds in a flower head (Sobhian and Pittara 1988). According to Sobhian and Pittara (1988), the overwintering generation passes the winter as mature larvae within cocoons made of pappus hairs inside the flower heads of *C. solstitialis*. The overwintering larvae pupate and emerge as adults the following spring in April and May. The first generation larvae develop primarily on *C. cyanus* as it typically flowers earlier than *C. solstitialis*; the second and third (overwintering) generation larvae develop on *C. solstitialis*.

Taxonomy, Host Range, and Geographic Distribution

The following information is from White and Marquardt (1989) unless otherwise specified. *Chaetorellia* is a Palearctic genus of nine known species in the tribe Terellinae. *Chaetorellia australis* is one of probably five *Chaetorellia* species in the *C. jaceae* species-group. *Chaetorellia australis* was originally described by Hering (1940) as a subspecies of *Chaetorellia hexachaeta* (Loew). The known hosts of all known species of *Chaetorellia* are species of *Centaurea, Carthamus* and *Chartolepis* in the Cardueae subtribe Centaureinae. The known hosts of species of *Chaetorellia* in the *C. jaceae* species-group are species of *Centaurea*. The host records for *C. australis* include *C. solstitialis* from Bulgaria, Greece, Hungary, Turkey and Moldavian SSR; *C. cyanus* from Greece and Hungary; and *C. depressa* Bieb. from Turkey. *Centaurea solstitialis* is in the subgenus *Solstitiaria*, and *C. cyanus* and *C. depressa* are in the subgenus *Cyanus* (Dostal 1976). In an extensive field sample of natural populations of a di-

Table 1. *Chaetorellia australis* no-choice host specificity tests in Albany, California, 1986–87.

Plant Species	Year Tested	No. of Plants Tested	Total Heads Tested	% Damaged Heads (with Frass, Larvae, Pupae or Pupal Cases)	% Heads with Frass Only	% Heads with Larvae, Pupae, or Pupal Cases
Centaurea solstitialis	1986	25	320	93.7	32.2	61.5
Centaurea solstitialis	1987	16	113	79.6	15.0	64.6
Centaurea cyanus	1987	20	268	85.8	1.5	84.3
Centaurea americana	1986	25	39	0	0	0
Centaurea rothrockii	1986	14	45	0	0	0
Carthamus tinctorius ("Hartman")	1986	25	72	0	0	0
Carthamus tinctorius ("4440")	1987	20	107	0	0	0
Cirsium occidentale	1986	25	73	0	0	0
Helianthus annuus	1986	25	68	0	0	0
Zinnia elegans	1986	13	145	0	0	0
Lactuca sativa	1986	20	800	0	0	0

verse array of thistles throughout mainland Greece in 1985, *C. australis* was reared only from the flower heads of *C. solstitialis* and *C. cyanus* (Turner et al. in press).

Host Specificity Testing

Host specificity was measured in no-choice cage tests of *C. australis* oviposition and development on nine test plant species. The adult flies used in all tests were collected in northeastern Greece (by R. Sobhian) as larvae in heads of *C. cyanus* and shipped to the USDA-ARS quarantine facility of the Biological Control of Weeds Laboratory at Albany, California. Tests were carried out in this quarantine facility during the summers of 1986 and 1987.

Host test plant species were chosen on the basis of taxonomic affinity, economic significance, and place of origin. The test plant species were *C. solstitialis, C. cyanus, C. americana* Nutt., *C. rothrockii* Greenm., two varieties of *Carthamus tinctorius* L., *Cirsium occidentale* (Nutt.) Jeps., *Helianthus annuus* L., *Lactuca sativa* L., and *Zinnia elegans* Jacq.. All test plant species are in the Asteraceae, and all are in the thistle tribe Cardueae except *H. annuus, L. sativa* and *Z. elegans. Carthamus tinctorius* (safflower) and *H. annuus* (sunflower) are oilseed crops, and *H. annuus* is native to the United States. *Carthamus tinctorius* var. "Hartman" is grown primarily in the northern plains area, while *C. tinctorius* var. "4440" was developed primarily for California. *Zinnia elegans* (zinnia) is an ornamental, and *L. sativa* (lettuce) is a leafy food crop. *Centaurea americana, C. rothrockii* and *C. occidentale* are thistles native to the United States. *Centaurea solstitialis* and *C. cyanus,* the known hosts, served as controls.

Test plants were grown in 15 cm pots and the plants of each species were arranged on a wood base platform (ca. 1 m^2) according to a random number table. The test plants were enclosed by 1 m^3 screen cages that rested on the wooden bases. One plant species was tested per cage. Thirteen to 25 plants were tested per plant species (Table 1). One pair (1♀ 1♂) of newly emerged files were used per test plant; for example 25 plants and 25 pairs of flies (50 flies total) were enclosed by a cage in the test with *C. americana* (Table 1). The flies were released into each cage where they had free access to the test plants. Food for the adult flies was provided by a 30 ml shell vial with a wick containing a honey-water solution. The tests were conducted under natural light conditions (14.5–16 h light; average of 24°C daytime and 13°C nightime). Tests were terminated when all adult female flies were dead, the longest last-

Table 2. Number of pupae per infested flower head in *Chaetorellia australis* no-choice host specificity tests in Albany, California, 1986–1987.

Plant Host Species (Year Tested)	No. Flower Heads Infested by Pupae	% Flower Heads with 1 Fly Pupa per Flower Head[1]	% Flower Heads with 2 Fly Pupae per Flower Head[1]
Centaurea solstitialis (1986)	143	92.3	7.7
Centaurea solstitialis (1987)	55	94.5	5.5
Centaurea cyanus (1987)	198	98.7	1.3

[1] Pupal counts include intact living pupae and pupal cases from emerged flies.

ing 36 days. The flower heads were then dissected and microscopically examined for evidence of *C. australis* feeding and development (frass, larvae, pupae or pupal cases). Tests were conducted between 18 June to 10 September 1986, and 15 June to 24 July 1987.

Results and Discussion

Oviposition and larval development occurred only on *C. solstitialis* and *C. cyanus*, and these species were heavily attacked as evidenced by the presence of frass, larvae, pupae or pupal cases. Next generation adult flies emerged only in the cages containing *C. solstitialis* and *C. cyanus*. There was no evidence of host use of any of the other test plant species. For *C. solstitialis*, 93.7% of the flower heads in 1986 and 79.6% of the flower heads in 1987 were attacked by the fly, while 85.8% of the *C. cyanus* flower heads were attacked (Table 1). Our results are congruous with the known host records (White and Marquardt 1989, Turner et al. in press). All available information indicates that *C. australis* has a narrow host range with *C. solstitialis*, *C. cyanus* and *C. depressa* as the only known hosts. The restricted host range of this fly provides strong evidence that it is safe for introduction into the United States as a biological control agent for yellow starthistle.

In the course of the flower head dissections, the numbers of pupae and pupal cases (from emerged flies) per flower head were noted. *Chaetorellia australis* does not appear to be gregarious as mostly only one or sometimes two pupae were found in infested flower heads (Table 2). For *C. solstitialis*, 92.3% (1986) and 94.5% (1987) of the infested flower heads had only one pupa, and 98.7% of the infested flower heads of *C. cyanus* had only one pupa (Table 2).

Acknowledgments

R. Sobhian collected the *C. australis* used in the host specificity testing. The California Department of Food and Agriculture provided funding support for this study. L. A. Andres and S. L. Clement critically reviewed the manuscript.

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TWO NEW SPECIES OF BLACK FLIES (DIPTERA: SIMULIIDAE) FROM NORTH AMERICA

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Abstract.—The larva, pupa, female, and male of two new species of black flies from North America are described and illustrated. ***Simulium fionae,*** new species, a member of the *S. vernum* group, is known from Pennsylvania and New Hampshire. ***Simulium claricentrum,*** new species, a member of the *S. pictipes* group, is known from Arkansas, Missouri, Oklahoma, and Pennsylvania. Characters are provided to separate both species from closely related Nearctic taxa.

Key Words: Simuliidae, *Simulium,* black fly, aquatic insect

As of 1986, the North American simuliid fauna north of Mexico consisted of 162 formally recognized species (Crosskey 1987); one additional species has since been described (Adler 1987). In the present paper, I describe two new Nearctic species, one a member of the *Simulium vernum* group and the other a member of the *S. pictipes* group.

The taxonomic status of the Nearctic *S. vernum* group has been summarized by Adler (1987). Thirteen species have been described formally, and the chromosomes of at least three additional species have been resolved in terms of the *vernum* standard (Brockhouse 1985, Hunter and Connolly 1986). Here, I describe all life stages of one of these latter species, *Simulium* sp. of Hunter and Connolly (1986). In the *S. pictipes* group, two species have been described (Shewell 1959) and a third, described herein, has been known cytologically as *S. pictipes* "A" (Bedo 1973, 1975).

Procedure and nomenclature follow those used by Adler (1987), although measurements of adults of *S.* sp. were taken from alcohol-preserved specimens and of *S. pictipes* "A" from freeze-dried specimens. What previously were referred to as mandibular teeth are differentiated in this paper as serrations and sensillum, following the terminology of Craig and Craig (1986). All illustrations and photographs are based on material collected at the type localities. Holotypes and some paratypes are deposited in the United States National Museum of Natural History, Washington, D.C. Additional paratypes are deposited in the Canadian National Collection, Biosystematics Research Centre, Ottawa (all chromosomal photographs are deposited here); the British Museum (Natural History), London; and the Clemson University Arthropod Collection, South Carolina.

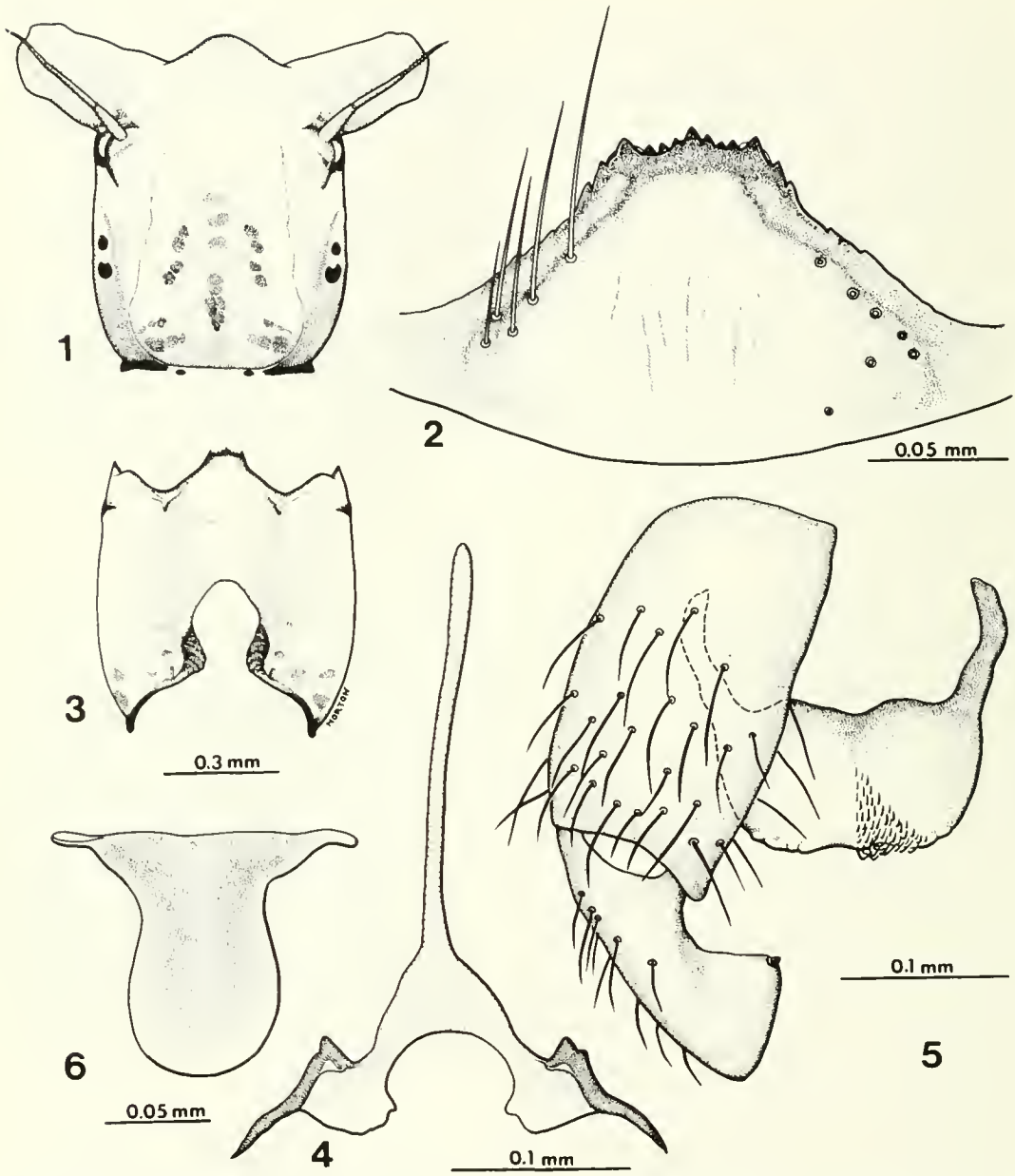
Simulium fionae Adler, NEW SPECIES
Figs. 1–9

Simulium (*Eusimulium*) *furculatum,* Adler, 1983, (not Shewell 1952): 197, pupa.

Simulium (*Nevermannia*) species near *furculatum/croxtoni* Adler & Kim, 1986: 29, larva, pupa.

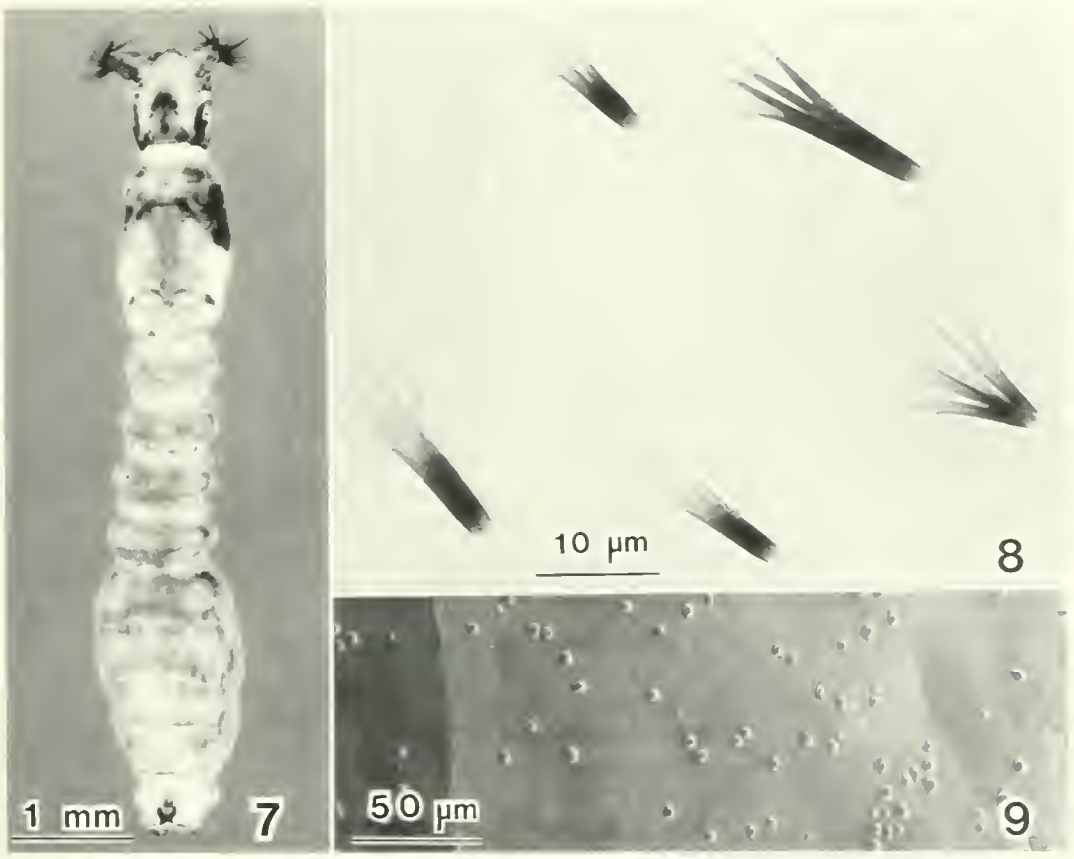
Simulium sp. Hunter & Connolly, 1986: 300, chromosomes.

Simulium sp. near *croxtoni-furculatum* Hunter, 1987: 52, chromosomes.



Figs. 1–6. *Simulium fionae* new species. 1, Larval head capsule (dorsal view). 2, Larval hypostoma. 3, Larval head capsule (ventral view). 4, Female genital fork (sternite 9). 5, Male terminalia (ventral view with left gonocoxite, gonostylus, and parameres removed). 6, Male dorsal plate.

Larva (final instar).—Length 6.3–7.5 mm ($\bar{x}$ = 6.8 mm, n = 47). Head capsule (Fig. 1) pale yellowish brown, palest anterodorsally, covered with numerous, fine, pale, simple setae (visible with phase contrast); headspots brown, distinct, delineating infuscated area; eye spots rather large; line over eye spots brown, leading into heavy



Figs. 7–9. *Simulium fionae* new species. 7, Larval habitus (dorsal view). 8, Larval cuticular setae (from dorsum of segment 7), as viewed with bright-field compound microscope. 9, Scanning electron micrograph of granules on portion of pupal thorax (dorsal view); ecdysial line is apparent on the left side.

brown area posteriorly. Antenna with distal article faintly brown, median article translucent or very pale yellowish brown dorsally, proximal article pale yellowish brown; approximately ⅓–½ of distal article surpassing labral-fan stalk; proportions of articles (distal to proximal, excluding apical sensillum) approximately 1.0:1.3:1.0. Labral fan with 41–51 ($\bar{x} = 46$, $n = 45$) primary rays in New Hampshire specimens [35–40 ($\bar{x} = 37$, $n = 2$) in Pennsylvania specimens]. Hypostomal teeth (Fig. 2) with median tooth and lateral teeth subequal in length and prominence; sublateral teeth variously smaller; lateral margin of hypostoma with 2 paralateral teeth and 2–5 lateral serrations per side; hypostoma with 2–3 prominent and 2–5 small lateral setae per side. Postgenal cleft (Fig. 3) about 1.3–1.5 times as long as wide, extending about ½–⅗ distance to hypostomal groove, widest at midpoint, rounded apically; subesophageal ganglion unpigmented. Maxillary palpus 2.8–3.5 times as long as basal width. Inner subapical ridge of mandible with double or triple sensillum proximal to 1 elongate serration. Lateral plate of thoracic proleg moderately sclerotized, rather broad, elongate, extending almost entire length of apical article. Body (Fig. 7) reddish brown; intersegmental bands clear, distinct; ventral tubercles rounded, about ⅓ depth of abdomen at attachment points; abdominal segments 4–8 (sometimes 5–8) dorsally and laterally with

many short, multiply branched, dark brown setae (Fig. 8), ventrally with similar but much sparser dark brown setae; thoracic and remaining abdominal segments with many shorter, multiply branched, translucent setae (visible with phase contrast). Anterodorsal arms of anal sclerite broadly connected to and subequal in length to posteroventral arms, associated with elongate, translucent, simple setae (visible with phase contrast). Rectal setulae pale, sparse (visible with phase contrast). Posterior proleg bearing 9–12 hooks in 61–64 rows. Anal papillae of 3 compound lobes.

Pupa.—Length 3.1–3.9 mm ($\bar{x}$ = 3.4 mm). Head projecting downward, with numerous, minute, rounded granules; antennal sheath of female extending almost to posterior margin of head; antennal sheath of male extending about ½ distance to posterior margin of head. Gill (Fig. 58 in Adler and Kim 1986) about as long as pupa, consisting of 8 rather widely splayed filaments; base short, giving rise to 3 short petioles; dorsalmost petiole giving rise to 2 widely divergent filaments; lateral petiole giving rise to a single lateral (or ventral) filament plus a dorsal pair on a petiole 1–5 times its basal width (rarely sessile); ventral petiole yielding a single lateral filament plus a ventral pair on a petiole 1–6 times its basal width (rarely sessile); filaments grayish, long, thin, tapering, with numerous furrows; surface sculpturing of base weakly differentiated. Thorax (Fig. 9) with numerous, minute, dome-shaped granules; trichomes simple (some occasionally bifid), slender, dark, 5–6 on each side of thorax. Tergite I with 1 pair of setae; tergite II with 5–6 anteriorly directed setae on each side of midline, and 1–2 minute setae laterally; tergites III and IV each with 4 anteriorly directed hooks on posterior margin on either side of midline, 1 small seta between and anterior to 2 outermost hooks, and 2–3 small setae laterally; tergites V to VIII each with row of fine, posteriorly directed spines along anterior margin, and 2–3 minute setae posteriorly on either side of midline; tergite IX with pair of short, stout, slightly curving, dorsally directed terminal spines. Pleural membrane of segments II to VII usually with 1–3 minute setae per side. Sternite III with about 3 minute setae per side; sternite IV posteriorly with pair of closely set, moderately heavy, simple or bifid, anteriorly directed setae, and at least 2 fine, minute setae per side; sternite V posteriorly with 1 pair of closely set, anteriorly directed, multifid, hook-like setae, and at least 1 pair of fine setae per side; sternites VI and VII posteriorly with 1 pair of distantly set, anteriorly directed, simple to trifid, hook-like setae, and at least 1 pair of fine setae per side; sternites VIII and IX with at most 1 pair of fine setae; sternites IV to VIII with numerous, extremely fine microspines. Cocoon (Fig. 41 in Adler and Kim 1986) well formed, rather coarsely woven, with short, irregularly woven anterodorsal projection accounting for about 4.6–13.9% ($\bar{x}$ = 9.3%, n = 9) total cocoon length (in lateral view).

Female.—General body color brown, with gray pruinosity, and silvery and pale golden pile. Length: body, 2.9–3.2 mm ($\bar{x}$ = 3.0 mm, n = 5); wing, 3.1–3.3 mm ($\bar{x}$ = 3.2 mm, n = 3).

Frons at vertex about 1.5–2.0 times broader than at narrowest point, about ⅙ width of head, with decumbent and erect, sparse, mixed silver and brown pile. Clypeus about as long as wide, with sparse silvery pile. Occiput with silvery pile reaching posterior margin of eye; postocular setae black. Antenna with fine silver pubescence; first flagellomere longest; pedicel and scape light brown; flagellum brown. Mandible with 41–45 serrations. Lacinia with 31–32 retrorse teeth. Palpus dark brown, with stout, pale golden setae; palpomere V 1.7–2.0 times as long as III. Sensory vesicle elongate, located posteriorly to subcentrally, occupying about ½ of palpomere III; neck short, arising near anterodorsal margin, opening to exterior through rounded, slightly expanded mouth. Median proximal space of cibarium broadly U-shaped, lacking armature.

Postpronotum and proepisternum brown,

with long silvery pile. Scutum dark brown, humeral angles light brown; pile recumbent, golden centrally, silvery peripherally. Scutellum dark brown, with long, very pale golden pile mixed with black setae. Postnotum dark brown. Anepisternum and katepisternum dark brown; katepisternum with a small, ventral patch of silvery pile (often rubbed off); membrane and mesepimeron brown; mesepimeral tuft of long, silvery setae. Wing veins pale yellowish brown. Setae on stem vein and costal base dark brown, with bronze reflections; setae on other veins primarily brown; subcosta setose ventrally; fringes of calypter and alar lobe silvery. Halter tan, with line of pale golden pile. Coxae and tarsi dark brown; femora and tibiae brown; pile on legs silvery to pale golden; hind basitarsus 6.5–7.3 times as long as broad; calcipala and pedisulcus well developed; claws each with large, thumb-like lobe.

Abdominal sclerites dark brown; pile sparse, silvery; additional sparse, long, black setae on terminal tergites; membranous areas gray to brown, with silvery pile. Basal fringe of long, silvery to very pale golden pile. Anal lobe subquadrate in lateral view, rounded anteriorly, with acute posterodorsal extension. Cercus a broadly rounded triangle, about 1.2–1.8 times as broad as long. Hypogynial lobes subtriangular, with space between lobes forming a narrow rectangle. Genital fork (Fig. 4) with stem moderately long and slender; lateral arms rather broad basally, forming suboval space in region of bifurcation; posteromedial areas of lateral arms well developed, and with bluntly acute angles; anteromedial area produced anteriorly. Spermatheca over 1.5 times as long as broad, with superficial pattern of subequal polygons.

Male.—General body color velvety black, with gray pruinosity and golden pile. Length: body 3.0–3.3 mm ($\bar{x}$ = 3.1 mm); wing, 2.7–2.9 mm ($\bar{x}$ = 2.7 mm).

Frons and clypeus with erect, brown pile. Occiput with long, erect, brown pile. Antenna dark brown, with fine, light brown pile. Palpus dark brown, with brown pile; palpomere V about twice as long as palpomere III. Sensory vesicle subspherical, about ⅙ length of its segment, located posteriorly; neck rather short, slender, opening to exterior through small, rounded mouth.

Postpronotum and proepisternum brown, with silvery to pale golden pile. Scutum velvety black, with recumbent, golden pile. Scutellum dark brown, with bronze pile. Postnotum dark brown. Anepisternum, katepisternum, membrane, and mesepimeron dark brown, latter two sometimes paler; katepisternum bare; mesepimeral tuft of long, brown pile with bronze reflections. Wing veins pale yellowish brown. Setae on stem vein and costal base dark brown; setae on other veins brown; fringes of calypter and alar lobe brown with bronze reflections. Halter dark brown basally, paler distally, with bronze pile. Legs dark brown, with midsections of femora and tibiae paler; pile brown and golden brown, sometimes silvery on forecoxa. Hind basitarsus 5.3–6.0 times as long as broad.

Abdominal tergites velvety black, paler along posterior margins, with bronze pile; membranous areas gray, with bronze pile; sternites dark brown, with bronze pile. Basal fringe of very long, bronze pile. Terminalia as in Fig. 5. Gonocoxite about as long as broad. Gonostylus about as long as gonocoxite, about 2.9 times as long as breadth at midpoint, expanded apically into flattened, subtriangular, medially directed flange bearing 1 apical spine. Ventral plate in ventral view subrectangular, about twice as broad as long, slightly narrowing posteriorly, with posterolateral corners well rounded, and posterior margin medially produced as a small, hirsute tubercle; anterior margin with slight, medial concavity; arms directed slightly outward, with apices bowed slightly inward; lip in terminal view pronounced, broadly rounded, serrate laterally; median sclerite long, slender, forked for about ¼–⅓ its length; dorsal plate (Fig. 6) well sclerotized, with broad collar-like base, suborbicular distally; paramere in lateral view moderately narrow basally, broad-

ening medially, and bearing 1 long, slender, strongly sclerotized spine-like process.

Chromosomes (from larval salivary glands; inversions are relative to the *S. vernum* standard of Brockhouse [1985], Hunter and Connolly [1986]; 20 preparations examined by Hunter and Connolly [1986] from Pennsylvania, 20 preparations examined from New Hampshire).—$n = 3$; chromocenter present; B chromosomes lacking; IS with inversions *IS-1, IS-4,* and *IS-5*; IL with inversions *IL-2, IL-3, IL-4, IL-6,* and *IL-7,* and with secondary nucleolar organizer (section 41C-42B) generally expressed; IIS standard for *vernum* sequence; IIL complexly rearranged (Fig. 18 in Hunter and Connolly 1986); IIIS with inversion *IIIS-2*; IIIL with inversions *IIIL-4, IIIL-5, IIIL-6,* and *IIIL-8*; sex chromosomes differentiated as Y_1 = IIIL-1 *sp,* X_0 = IIIL standard; floating inversions in all arms except IIIS.

Types.—Holotype: ♂ (pinned) with pupal and larval exuviae (in glycerin), outlet, Two-Towns Pond, Dixville Notch (The Balsams), Coos County, New Hampshire (44°52′N, 71°18′W), 24 May 1988, collected by P. H. Adler. Paratypes: NEW HAMPSHIRE: COOS COUNTY: same data as holotype, 77 larvae (including 40 mature), 10 chromosome preparations (8 female larvae, 2 male larvae) with photographic negatives, 15 pupae, 1 pupal exuviae, 4 ♂ (pinned) with larval and pupal exuviae (in glycerin), 1 ♂ (cleared, in glycerin), 3 ♀ (pinned) with larval and pupal exuviae (in glycerin); same data as holotype, 19 May 1987, 2 larvae, J. F. Burger; same data as holotype, 26 May 1987, 8 larvae, 4 chromosome preparations (3 female larvae, 1 male larva) with photographic negatives, J. F. Burger; outlet, beaver pond no. 5, Dixville Notch (The Balsams), 20 May 1987, 1 larva, 1 chromosome preparation (female larva) with photographic negatives, J. F. Burger; PENNSYLVANIA: MONROE COUNTY: outlet, White Heron Lake, Rt. 402, 1.6 km north of Marshalls Creek (town), 7 May 1983, 4 larvae, 1 pupa, P. H. and C. R. L. Adler.

Additional specimens examined.—PENNSYLVANIA: MONROE COUNTY: pond outlet, Pocono Highland Camp, Rt. 402, 4.8 km north of Marshalls Creek (town), 7 May 1981, 1 pupa, G. E. Jones; NEW HAMPSHIRE: COOS COUNTY: outlet, Round Pond, Dixville Notch (The Balsams), 9 June 1988, 4 larvae, J. F. Burger.

An additional 83 males (68 pinned with exuviae in glycerin, 15 in alcohol with exuviae) and 43 females (34 pinned with exuviae in glycerin, 9 in alcohol with exuviae) were examined from the type locality (same data). Based on the configuration of the pupal gill, these specimens appear to be *S. fionae.* However, because pupal characters exhibit overlap between *S. fionae* and *S. croxtoni* and because the larval cuticle did not remain associated, I labeled the specimens as *Simulium croxtoni/fionae.*

Etymology.—This species is named in honor of Fiona F. Hunter who originally resolved the chromosomes of this species, and who has contributed significantly to a cytological understanding of the *S. vernum* group.

Diagnosis.—The larva of *S. fionae* is easily distinguished by the dark, multiply branched setae covering the posterior 4 or 5 abdominal segments. Larvae of the closely related and morphologically similar *S. croxtoni* Nicholson and Mickel possess dark, simple abdominal setae and generally have a longitudinal, pale brown stripe on the frontoclypeal apotome. Larvae of *S. furculatum* Shewell have simple setae and some scattered, multiply branched (mainly bifid) setae. The pupal gill of *S. fionae* is generally darker and more splayed than in *S. croxtoni* and *S. furculatum,* and the single filament of the ventral petiole typically arises lateral to the doublet, whereas in *S. croxtoni* the doublet often arises lateral to the single filament. The anterodorsal projection of the

cocoon is often shorter than in *S. croxtoni*. No reliable characters have been found to distinguish females of *S. fionae* and *S. croxtoni*. In *S. fionae*, the ventral plate of the male is slightly broader and less tapered than in *S. croxtoni*.

Chromosomally, *S. fionae* differs from the *S. vernum* standard by approximately 23 fixed inversions, and from all other known species by at least one fixed inversion in every arm except IIS (Hunter and Connolly 1986). It is most readily distinguished by a chromocenter in combination with a subterminal Z marker (section 32A–32B) and a reoriented blister group (sections 75C–76A), relative to standard. Populations in New Hampshire and Pennsylvania both carry IL-1 *sp*, IIL-1 *sp*, IIL-2 *sp*, and the simple Y-linked inversion IIIL-1 *sp*. Larvae from New Hampshire sporadically carry a small inversion in the middle of IS, two independent inversions in IIS (approximate limits 52–54 inclusive and 50–52C inclusive), and a subterminal inversion in IIL (approximate limits 71B–72C2 inclusive). Additionally, the majority (85%, $n = 20$) of New Hampshire larvae carry at least one of five inversions in IL.

Biology.—*Simulium fionae* was collected from the outlets of two man-made impoundments in Pennsylvania and from the outlets of two beaver ponds and one man-made impoundment in New Hampshire. In Pennsylvania, larvae and pupae were collected in early May from old cattail (*Typha*) leaves and stalks trailing in the water. In New Hampshire, immatures were found from mid-May to early June almost exclusively on the undersurfaces of stones and sticks. At all sites, immatures were found with *Cnephia dacotensis* (Dyar and Shannon), and were restricted to within 20 m of the outlet. Stream temperatures at the time of collection ranged from 16.5 to 17°C, and stream widths ranged from 0.6 to 1.2 m. Nearly 12% of the larvae collected at the Two Towns Pond outlet were infected with mermithid nematodes; one larva was infected with the fungus *Coelomycidium simulii* Debaisieux while another was infected with an unidentified microsporidium.

Simulium claricentrum Adler, New Species

Figs. 10–17

Simulium pictipes "A" Bedo, 1973: 12, chromosomes.

Simulium "species A" Reisen, 1974a: 19, ecology.

(*Hagenomyia*) "species A" Reisen, 1974a: 72, larval biology.

Simulium "species A" Reisen, 1974b: 275, larval biology.

Simulium (*Shewellomyia*) "species A" Reisen, 1975a: 949, larval biology.

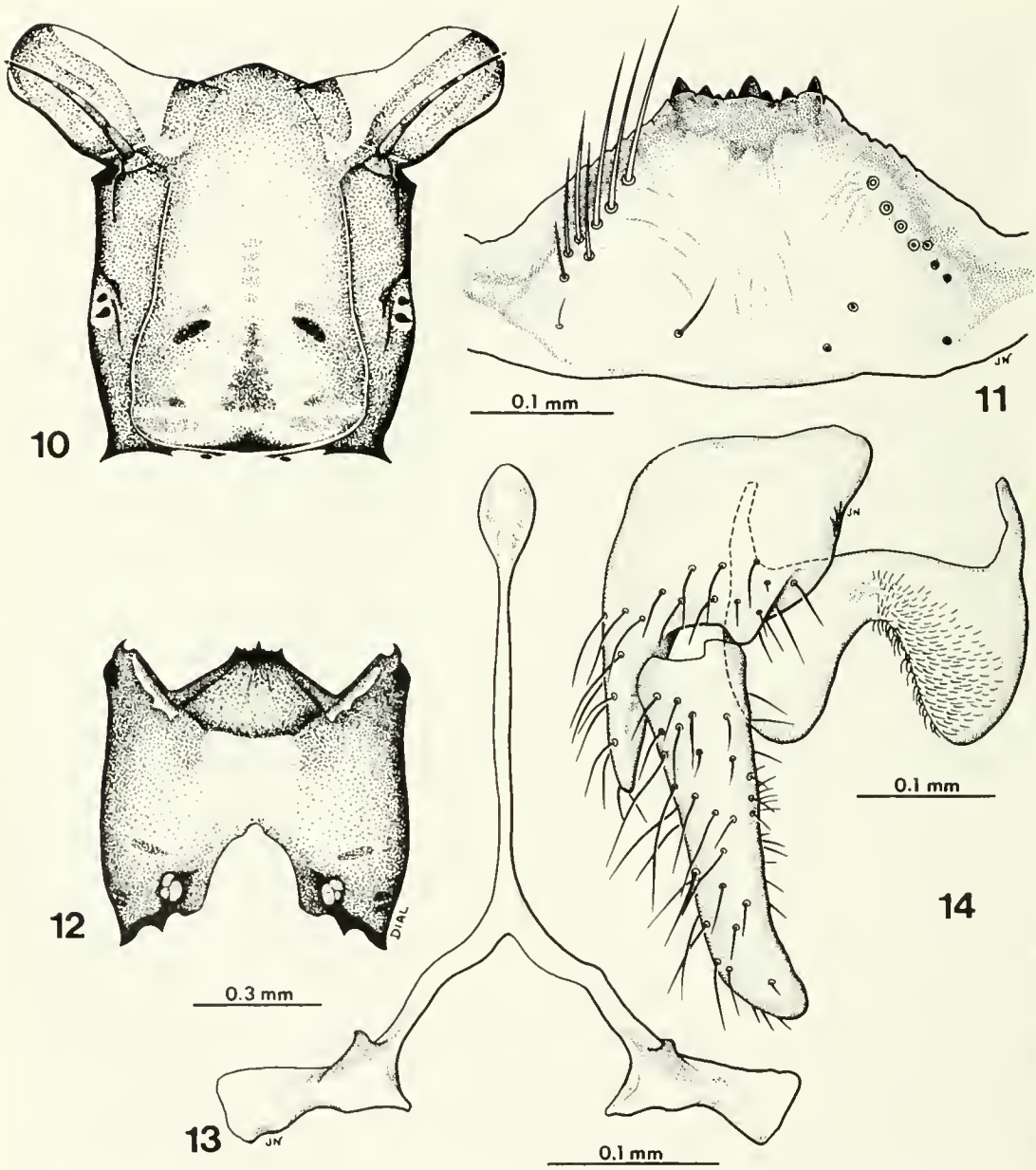
Simulium "sp. a." Reisen, 1975b: 27, larval biology.

Simulium pictipes "A" Bedo, 1975: 1150, chromosomes.

Simulium (*Shewellomia*) [sic] "species A" Reisen, 1977: 325, larval ecology.

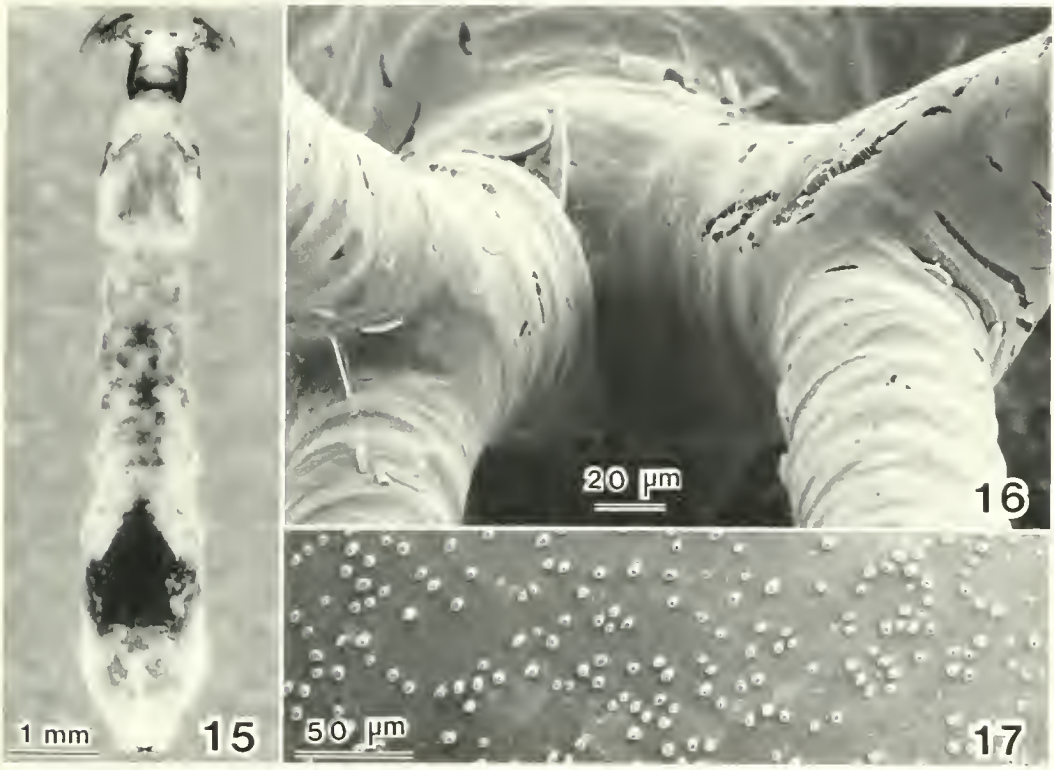
Simulium (*Shewellomyia*) *pictipes* "cytospecies A" Adler and Kim, 1986: 36, larva.

Larva (final instar).—Length 7.2–9.9 mm ($\bar{x} = 8.5$ mm, $n = 47$). Head capsule (Fig. 10) whitish yellow to brown with pale areas centrally and anteriorly on frontoclypeal apotome; pigmentation beneath cuticle often visible as dark reticulate pattern; headspots indistinct, or with anterolateral, posterolateral, and/or posteromedian headspots brown, fairly distinct; eye spots rather large; line over eye spots thin, brown. Antenna with distal article brown, median article pale brown (hyaline band visible subapically in darker specimens), proximal article pale brown; apex of distal article reaching end of labral-fan stalk; proportions of articles (distal to proximal, excluding apical sensillum) approximately 1.0:1.7:1.0. Labral fan with 47–60 ($\bar{x} = 54$, $n = 45$) primary rays. Hypostomal teeth (Fig. 11) with median tooth and lateral teeth relatively large; me-



Figs. 10–14. *Simulium claricentrum* new species. 10, Larval head capsule (dorsal view). 11, Larval hypostoma. 12, Larval head capsule (ventral view). 13, Female genital fork (sternite 9). 14, Male terminalia (ventral view with left gonocoxite, gonostylus, and parameres removed).

dian tooth longest; outermost sublateral teeth shorter than lateral teeth, but longer than innermost sublateral teeth; median sublateral teeth shortest; lateral margin of hypostoma with 0–2 small paralateral teeth and 3–4 lateral serrations per side; hypostoma with 6–7 prominent setae and 1–2 small lateral setae per side. Postgenal cleft (Fig. 12) about as long as basal width, extending about ½ distance to hypostomal



Figs. 15–17. *Simulium claricentrum* new species. 15, Larval habitus (dorsal view). 16, Scanning electron micrograph of base of pupal gill. 17, Scanning electron micrograph of granules on portion of pupal thorax (dorsal view).

groove, widest at base, narrowing anteriorly to rounded point; subesophageal ganglion darkly pigmented. Maxillary palpus 3.2–4.0 times as long as basal width. Inner subapical ridge of mandible with single sensillum proximal to 1 large, subtriangular serration. Lateral plate of thoracic proleg moderately well sclerotized, about as long as wide, extending almost length of apical article. Body (Fig. 15) gradually expanding posteriorly, dark gray and white, piebald, lacking conspicuous cuticular setae; pigmentation heaviest on dorsum of segments 5–7 (often forming a triangle with apex pointing anteriorly), and on thorax; gonadal sheath darkly pigmented in male (often visible through integument), unpigmented or pigmented posteriorly in female. Anterodorsal arms of anal sclerite broadly connected to, broader than, and about ⅓ shorter than posteroventral arms. Rectal setulae short, sparse, visible only under phase contrast. Posterior proleg bearing 18–22 hooks in 92–100 rows. Anal papillae of 3 compound lobes.

Pupa.—Length 3.3–4.5 mm ($\bar{x}$ = 3.9 mm, n = 15). Head projecting downward, with many minute granules as on thorax; antennal sheath of female extending nearly to posterior margin of head; antennal sheath of male extending about ½ distance to posterior margin of head. Gill short, about ⅓ length of pupa, consisting of 9 filaments; base extremely short, immediately giving rise to 4 short-petiolate pairs of filaments plus a single filament that curves ventrolaterally and often wraps around head; filaments moderately thin, tapering, weakly

annulate; surface sculpture of base weakly differentiated (Fig. 16). Thorax with numerous, irregularly spaced, minute, rounded granules (Fig. 17); trichomes simple, moderately long, slender, rather dark, 7 on each side of thorax. Tergite I with 1 pair of setae; tergite II with 4 stout, anteriorly directed setae and 3 smaller setae on each side of midline, plus 3 setae laterally per side; tergites III and IV each with 4 anteriorly directed hooks on posterior margin on either side of midline, 2 small setae between and anterior to 2 outermost hooks, and 3–4 small setae laterally per side; tergites V to VII bare or with 1 minute seta each; tergite VIII with 3–6 hook-like setae along anterior margin on each side of midline, plus 2 minute setae per side and numerous comb-like microspines laterally; tergite IX with pair of very short, stout, slightly curving, dorsally directed terminal spines, and numerous comb-like microspines. Pleural membrane of segments II to VII with 0–1 minute setae per side. Sternite III with pair of fine setae; sternite IV with 2–3 heavy, anteriorly directed setae and 1–2 fine setae per side; sternite V with pair of stout, anteriorly directed setae and 2 fine setae per side; sternites VI and VII with pair of long, anteriorly directed, hook-like, simple or bifid setae and 1–2 fine setae per side; sternites VIII and IX generally lacking setae; sternites III to VIII with numerous rows of extremely fine, comb-like microspines. Cocoon boot-shaped, covering entire pupa and gill, very coarsely woven (especially anteriorly).

Female.—Generally grayish pruinose, with black markings on thorax and abdomen; pile silver, more golden centrally on thorax. Length: body, 2.5–2.9 mm ($\bar{x}$ = 2.8 mm, n = 7); wing, 3.3–3.7 mm ($\bar{x}$ = 3.4 mm, n = 7).

Frons gray, at vertex about 1.5 times broader than at narrowest point, about ⅓ width of head, with decumbent, silver pile. Clypeus gray, slightly wider than long, with silver pile. Occiput with long, silver pile reaching posterior margin of eye; postocular setae black. Antenna with fine silver pubescence; first flagellomere longest, slightly longer than pedicel; scape and pedicel yellowish brown; flagellum dark brown. Mandible with 33–35 serrations. Lacinia with 26–27 retrorse teeth. Palpus dark brown, with stout, brown setae; palpomere V 1.9–2.3 times as long as III. Sensory vesicle located posteriorly, occupying about ½ of palpomere III, opening directly to exterior through rounded, expanded mouth (neck extremely short or lacking). Median proximal space of cibarium broadly U-shaped, lacking armature.

Postpronotum and proepisternum gray, with long silver pile. Scutum gray to grayish black, with 3 fine, black vittae running longitudinally, and with black patch anterodorsal to wing base; pile recumbent, silver, becoming golden centrally; humeral angle yellowish gray. Scutellum dark brown to grayish black, with long, mixed silver and brown pile. Postnotum dark brown. Anepisternum and katepisternum dark brown, with gray pruinosity; membrane and mesepimeron slightly paler; mesepimeral tuft of long, silver setae. Wing veins pale yellowish brown. Setae on stem vein and costal base mixed brown and silver; setae on other veins brown; subcosta setose ventrally; fringes of calypter and alar lobe silver. Halter tan to pale yellow, with line of fine, pale golden pile. Legs brown, often with paler patches, especially on hind basitarsus; pile primarily silver, brown on tarsi; hind basitarsus 6.4–7.7 times as long as greatest width; calcipala small; pedisulcus deep; claws simple, moderately curved.

Abdomen gray, with segments 3–5 black dorsally and segments 3–7 (sometimes 2) with small, partially shiny, brown patches laterally; sclerites of segments 6–9 dark brown, with gray pruinosity, and sparse, silver pile; sternite 7 with long, brown setae along posterior margin. Basal fringe of very long, silver pile. Anal lobe brown, shiny, subrectangular in lateral view, with ventral margin rounded, and with dorsal finger-like

extension nearly as long as body of lobe. Cercus subrectangular, about twice as broad as long, posterior margin straight, corners well rounded. Hypogynial valve a short truncate lobe, space between lobes rather broad, subrectangular. Genital fork (Fig. 13) with stem moderately long, slender, expanded at anterior end; lateral arms narrow, forming suboval to subtriangular space between them, posterior areas expanded into subrectangular plates. Spermatheca rather small, subspherical, with cuticular microspines.

Male.—Generally velvety black, with golden and brown pile. Length: body, 2.7–3.5 mm ($\bar{x}$ = 3.0 mm, n = 5); wing, 2.9–3.1 mm ($\bar{x}$ = 3.0 mm, n = 7).

Frons and clypeus with golden-brown pile. Occiput with long, erect, brown pile. Antenna brown, with fine, pale golden pubescence; pedicel pale brown. Palpus brown, with brown pile; palpomere V 2.5–2.7 times as long as palpomere III. Sensory vesicle oblong, about ¼ length of its segment; neck short, opening to exterior through rounded mouth.

Postpronotum and proepisternum brown, with long, silver pile. Scutum velvety black, with pair of silvery patches extending from humeral angle posteromedially, and with silvery patch posteriorly, humeral angles pale brown; pile recumbent, golden. Scutellum dark brown, with mixed brown and golden pile. Postnotum dark brown. Anepisternum, katepisternum, and membrane dark brown; mesepimeron dark brown, paler centrally; mesepimeral tuft of silver or pale golden pile. Wing veins pale gray to yellowish brown. Setae on stem vein and costal base dark brown; setae on other veins brown; fringes of calypter and alar lobe brown. Halter dark brown basally, tan to yellow distally, with fine, brown pile. Legs brown, with paler patches, especially on hind basitarsus; pile brown to golden brown. Hind basitarsus 4.9–5.0 times as long as broad; calcipala small; pedisulcus deep.

Abdominal tergites velvety black, with reflective, silver patches laterally on segments 2, 6, and 7, and minimally on 8; pile brown to golden brown; membranous areas grayish, with long, brown and golden brown pile; sternites brown, with brown pile. Basal fringe of long brown to golden brown pile. Terminalia as in Fig. 14. Gonocoxite about 1.5 times longer than broad, with ventrolateral angle produced posteriorly. Gonostylus narrow, rounded apically, about as long as gonocoxite, 3.6–3.7 times as long as basal breadth, lacking apical spinule. Ventral plate finely setose, in ventral view deeply and broadly incised posteromedially, about 1.5 times broader than long, with lateral margins somewhat parallel and anterior margin smoothly convex; arms short, with apices curving inward; lip in terminal view with three, subequally prominent lobes; median sclerite elongate, triangular; paramere in lateral view subquadrate basally, narrowing distally, and bearing numerous, variably long, spine-like processes.

Chromosomes (from larval salivary glands; Bedo 1975).—n = 3; chromocenter absent; pseudochromocenter (ectopic pairing) occasional; B chromosomes lacking; centromere regions of all chromosomes expanded, each bearing sharp centromere band (that of chromosome III included in heavily staining heterochromatic area of expanded region); all chromosome arms standard for *S. pictipes* group; IIL as sex chromosome, with females homozygous for heavy band at 63A4 and males heterozygous for heavy and thin band at 63A4; floating inversions lacking.

Types.—Holotype: ♂ (pinned) with pupal exuviae and larval head capsule (in glycerin), Sixteenmile Creek, junction of Washington Street and Shadduck Road, Northeast (town), Erie Co., Pennsylvania (42°11′N, 79°50′W), 10 August 1988, collected by P. H. Adler and C. R. L. Adler. Paratypes: same data as holotype, 174 larvae (including 40 mature), 10 chromosome preparations (6 female larvae, 4 male larvae) with photographic negatives, 36 pupae,

91 pupal exuviae, 24 ♂ (pinned) with exuviae (in glycerin), 2 ♂ (cleared, in glycerin), 2 ♂ (in alcohol), 25 ♀ (pinned) with exuviae (in glycerin); same data as holotype, 5 August 1986, 36 larvae, E. C. Masteller; ARKANSAS: MARION COUNTY: same data as holotype, 12 August 1989, 36 larvae (including 20 mature), 42 pupae. Georges Creek, junction of Rt. 62, 6 km west of Yellville, 24 April 1989, 9 larvae (including 1 mature), 5 pupal exuviae, P. H. Adler and C. R. L. Adler.

Additional specimens examined.—PENNSYLVANIA: ERIE COUNTY: Fourmile Creek, Wesleyville, near Behrend Campus, 12 May 1983, 1 chromosome preparation (female larva), E. C. Masteller.

Etymology.—The specific name is derived from the Latin *clari* meaning clear, and *centrum* meaning center, in reference to the clearly defined centromere bands that readily distinguish this species from closely related taxa.

Diagnosis.—Larvae (later instars) of *S. claricentrum* can be distinguished from those of other members of the *S. pictipes* group by the piebald pigmentation of the body and the paler head capsule; earlier instars are more uniformly dark. The nine-filamented gill of the pupa lacks the tuberculate surface sculpture on the basal ¼ to ⅓ of each filament, unlike other members of the *S. pictipes* group. The female cannot be reliably distinguished from that of *S. pictipes*. The ventral plate of the male is about 1.5 times as broad as long, with somewhat parallel lateral margins; in *S. pictipes* Hagen the ventral plate has divergent lateral margins, and in *S. longistylatum* Shewell it is nearly as broad as it is long. Chromosomally, the species is most easily identified by the presence of well-defined centromere bands (Bedo 1975).

Biology.—Like other members of the *S. pictipes* group, the immatures of *S. claricentrum* are often found in moss-like clumps in swift watercourses. In the Lake Erie drainage basin of Pennsylvania, *S. claricentrum* was found where water spilled over small shale-bottomed waterfalls, but in one case was found on a coarse cement sluiceway. These streams ranged in width from 10 to 20 m and in temperature from 16 to 27°C. In Oklahoma, *S. claricentrum* was collected from limestone streams with smooth, travertine substrates (Reisen 1974a, 1975a); larval abundance was highest during the spring months and was positively correlated with periphyton abundance (Reisen 1977). The Oklahoma streams ranged in temperature from 17 to 29°C, in pH from 7.7 to 8.2, in alkalinity from 235 to 250 ppm, and in dissolved oxygen from 7.5 to 8.5 ppm (Reisen 1974b, 1975a). In Arkansas, immatures were taken from a calcareous siltstone-bottomed stream approximately 10 m wide, with a temperature of 23°C. *Simulium claricentrum* is multivoltine, immatures having been collected from early May through August in Pennsylvania and year round in Missouri and Oklahoma (Bedo 1975, Reisen 1974a, 1975a, b). The species passes through six larval instars (Reisen 1975a). In 1989, I found a mixed population of *S. pictipes* and *S. claricentrum* in Sixteenmile Creek, Pennsylvania. About 5% of *S. claricentrum* larvae in Sixteenmile Creek (1989) carried patent infections of the microsporidium *Polydispyrenia simulii* (Lutz and Splendore), formerly known as *Pleistophora multispora* (Strickland) (Canning and Hazard 1982).

Reisen (1974a) recorded mating swarms at the base of riffles; coupled pairs immediately dropped to the ground where copulation lasted only a matter of seconds. Females oviposited from 200 to 400 eggs in dense masses during the early evening hours on rocks, grasses, algae, and mosses splashed with water (Reisen 1974a).

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J. F. Burger provided collections of *S. fionae* from northern New Hampshire, and facilitated my efforts to collect this species. E. C. Masteller provided the first Pennsyl-

vania collection of *S. claricentrum*, as well as several subsequent larval collections. F. F. Hunter scored three slides of *S. fionae* for polymorphisms. A. H. Undeen identified the microsporidia. C. I. Dial and J. P. Norton rendered the illustrations, and J. R. Brushwein and J. D. Culin photographed the larvae. C. R. L. Adler and J. C. Morse reviewed the manuscript. To all of these individuals I extend my thanks. This is Technical Contribution No. 2975 of the South Carolina Agricultural Experiment Station, Clemson University.

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NEW SPECIES AND RECORDS OF PREDACEOUS MIDGES FROM FIJI (DIPTERA: CERATOPOGONIDAE)

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Abstract.—Fourteen species of predaceous midges of the tribes Ceratopogonini, Heteromyiini, Sphaeromiini, and Palpomyiini are reported from Fiji, including eight species described as new: ***Downeshelea stenochora***, ***Monohelea beaveri***, ***M. fijiensis***, ***M. coloisuvae***, ***M. leveri***, ***Stilobezzia browni***, ***Nilobezzia fijiensis***, and ***Bezzia vitilevuensis***. All are new records from Fiji, from which only four species of Forcipomyiinae and two species of Culicoidini had previously been reported.

Key Words: predaceous midges, Ceratopogonidae, Fiji

The biting and predaceous midges of the family Ceratopogonidae are a conspicuous element of the Dipterous fauna of the Pacific islands. Tokunaga and Murachi (1959) recorded 147 species from Micronesia. For unknown reasons practically no collecting or taxonomic study has been done on the ceratopogonids of Fiji. Debenham (1978) made a careful listing of all the species recorded from the Australasian Region and recorded only six species from Fiji, as follows: *Atrichopogon jacobsoni* (de Meijere), *Forcipomyia fijiensis* (Macfie), *F. fuliginosa* (Meigen), *F. indecora* Kieffer, *Culicoides belkini* Wirth and Arnaud, and *C. cancrisocius* Macfie.

In this paper we report on the predaceous species of the tribes Ceratopogonini, Heteromyiini, Sphaeromiini and Palpomyiini. The species of the subfamilies Forcipomyiinae and Dasyheleinae, and the bloodsucking species of the tribe Culicoidini of the subfamily Ceratopogoninae will be reported on in a second paper. We here record 14 species, of which eight are new species, and all are new Fijian records.

Taxonomic characters employed for identification of adult ceratopogonids were described by Wirth et al. (1977), Downes and Wirth (1981), and particularly for the tribe Ceratopogonini by Wirth and Grogan (1988). Wing length is measured from the basal arculus to the wing tip and costal length from the basal arculus to the costal apex. Costal ratio is the costal length divided by the wing length. Antennal ratio of the female is the sum of the lengths of the elongated five distal flagellar segments divided by the sum of the lengths of the preceding eight; in the male the antennal ratio is the sum of the lengths of the elongated three distal segments divided by the sum of the lengths of the preceding 10 short segments. Palpal ratio is the length of the third palpal segment divided by its greatest breadth. Tarsal ratio is the value obtained by dividing the length of the basitarsus by the length of the second tarsomere.

The holotypes and allotypes of the new species herein described are deposited in the U.S. National Museum of Natural History in Washington, D.C. (abbreviated USNM).

Paratypes as available will be deposited in the British Museum (Nat. Hist.), London; the Museum National d'Histoire Naturelle in Paris; the Bishop Museum in Honolulu (BISH); the Australian National Insect Collection in Canberra; and the DSIR National Insect Collection in Auckland, New Zealand.

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Howard Moore, Technical Assistant at Loyola College, gave invaluable aid in the photographic work.

Subfamily Ceratopogoninae
Tribe Ceratopogonini
Genus *Alluaudomyia* Kieffer

References: Tokunaga, 1959 (New Guinea species); Tokunaga and Murachi, 1959 (Micronesian species); Wirth and Delfinado, 1964 (revision Oriental species); Debenham, 1971 (revision of Australia and New Guinea species).

Alluaudomyia bipunctata Tokunaga and Murachi

Alluaudomyia bipunctata Tokunaga and Murachi, 1959: 356 (male, female; Caroline Islands; fig. male wing, palpus, antenna, genitalia).

Distribution.—Caroline Islands; Fiji.

New record.—FIJI: Viti Levu, Savura Creek, v.1983, R. A. Beaver, Malaise trap, 2 females.

Alluaudomyia tenuistylata Tokunaga

Alluaudomyia tenuistylata Tokunaga, 1959: 296 (male; West Irian); Tokunaga, 1963: 225 (male, female; West Irian, New Guinea); Debenham, 1971: 171 (male, female redescribed; figs.; Queensland).

Distribution.—Fiji, New Guinea, Queensland, West Irian.

New record.—FIJI: Viti Levu, Savura Creek, v.1983, R. A. Beaver, Malaise trap, 2 females; 14 km w Lami, 7–10.xii.1986, R. L. and B. B. Brown, UV light trap, 1 male, 2 females.

Genus *Downeshelea* Wirth and Grogan

Downeshelea Wirth and Grogan, 1988: 50. Type-species, *Monohelea stonei* Wirth, by original designation.

References (to *Downeshelea* and *Monohelea*): Tokunaga and Murachi, 1959: 404 (Micronesian species); Tokunaga, 1963: 238 (New Guinea species); Debenham, 1972: 1 (Australia and New Guinea species); Ratanaworabhan and Wirth, 1972: 439 (Oriental species).

***Downeshelea stenochora* Wirth and Giles, New Species**

Figs. 1–7, 51

Female allotype.—Wing length 1.02 mm; breadth 0.39 mm.

Head: Brownish, narrow bases of antennal segments 4–10 pale. Eyes contiguous in a point, bare. Antenna (Fig. 3) with lengths of flagellar segments in proportion of 18-15-14-14-13-13-13-13-22-23-23-23-30; antennal ratio 1.17. Palpus (Fig. 4) dark brown, stout; lengths of segments in proportion of 4-8-14-9-13; palpal ratio 1.7. Mandible with 10 coarse teeth.

Thorax: Dark brown, scutellum yellowish on each end. Legs (Fig. 1) brown, paler on fore leg, dark brown on hind leg; knees conspicuously yellowish; hind femur and tibia slightly stouter. Hind leg with lengths from femur to tarsomere 5 as 88-78-50-20-10-9-12; hind basitarsus (Fig. 2) with abrupt bend near base, with one dense row of short palisade setae and a sparse row of longer setae, one strong black ventral spine at base and two slender spines at apex; tarsomeres 2–3 each with pair of slender apical spines; tarsomere 4 subcylindrical, with pair of long, strong, black spines at apex; hind claw single, simple, length 0.068 mm. Fore tarsus with slender ventral spines as follows: tarsomere 1 with one at base and two at apex; tarsomeres 2–4, one apical. Mid basitarsus with two similar spines at base and eight along length of segment; segments 2–4 each with two apical. Fore and mid claws paired, subequal, curved; elongate, length 0.043 mm on fore leg and 0.036 mm on mid leg. Wing (Fig. 51) with conspicuous pattern due to enlarged dark gray microtrichia consisting of a broad fascia across midlength at level of first radial cell, and a small subapical fascia in cell R5 behind tip of costa, the two connected by a darkened area in cell M1. Costa unusually elongate, costal ratio 0.85; two radial cells, the first nearly half the length of second, rather broad, the second unusually narrow, almost slitlike distally. Halter intensely dark brown.

Abdomen: Dark brown; pleural membrane with microscopic striations due to rows of dense blackish spicules. Spermathecae (Fig. 5) two, subspherical with well-developed stout necks; subequal, each 0.065 by 0.038 mm including the neck.

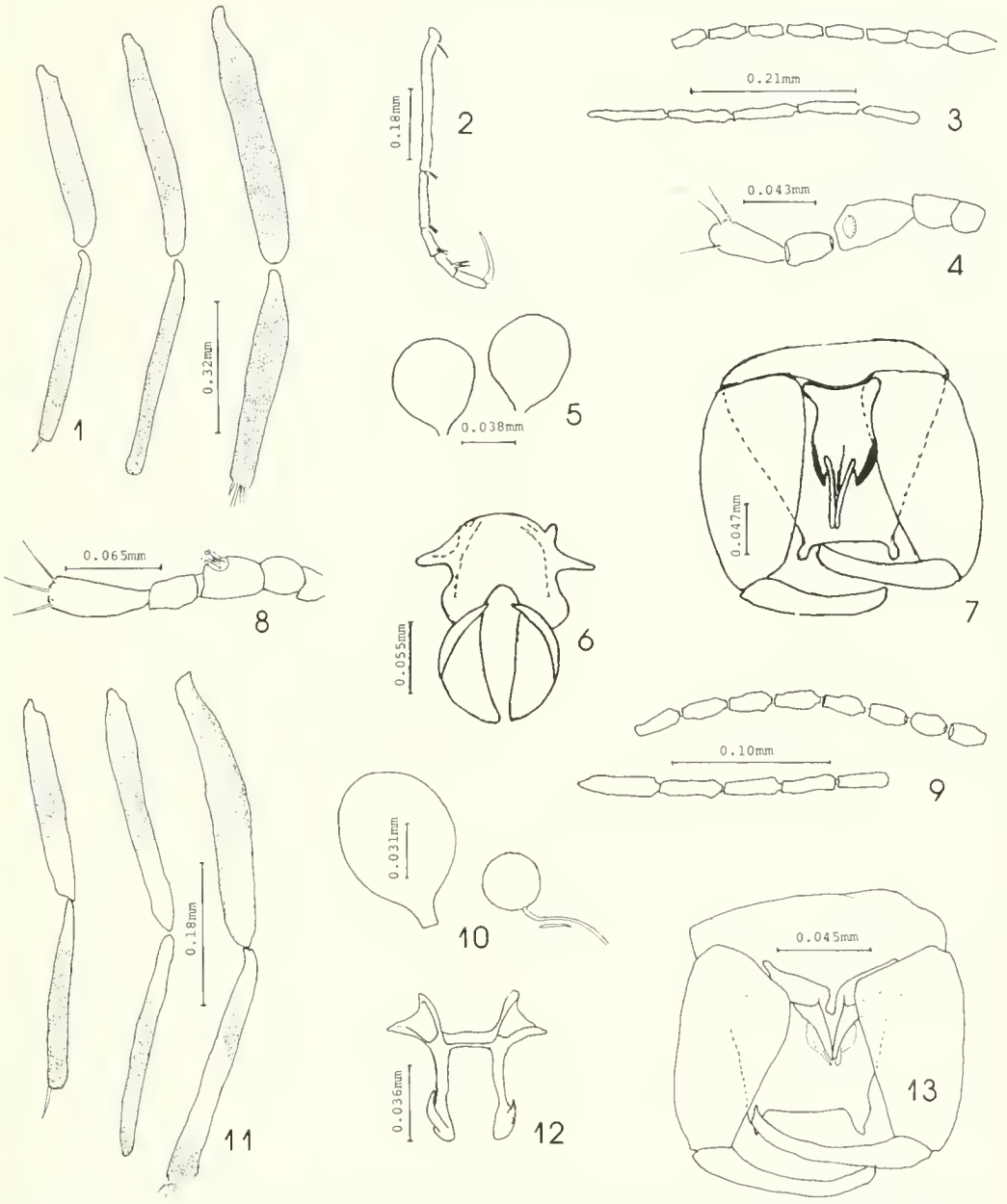
Male holotype.—Wing length 0.98 mm; breadth 0.29 mm.

Similar to the female with the usual sexual differences. Wing much narrower, costa shorter, CR 0.72. Antenna with well-developed, pale brownish plume; lengths of flagellar segments in proportion of 28-10-10-10-10-10-10-8-8-12-27-25-26, antennal ratio 0.87. Hind leg with lengths from femur to tarsomere 5 as 77-64-40-20-12-8-10. Claws short, equal and similar on all legs, each bent at base and straight distally.

Genitalia (Fig. 7): Dark brown, strongly sclerotized, about as long as broad. Ninth sternum narrow, slightly broadened caudad in midportion, there with four strong setae; ninth tergum convex distally, caudal margin nearly straight, with a pair of small, beadlike, apicolateral processes, each with a minute seta. Basistyle stout, about twice as long as broad, without lobes or armament; dististyle 0.65 as long as basistyle, moderately stout distally, slightly curved. Aedeagus complex, typical of the genus; basally a broad median plate about half again as long as broad, with a pair of short, stout, anterolateral arms, distolateral corners of the plate strongly sclerotized, flangelike; on the concave caudal margin of this plate between the flanges arise a pair of long slender processes nearly as long as the plate, with tips converging caudally on midline. Parameres (Fig. 6) joined on proximal third in a sclerotized plate with irregular outlines as figured, posteriorly expanded in a pair of broad, crescent-shaped processes, each bearing at broadest point on lateral margin a curved blade directed ventromesally with apices nearly meeting on midline at about half the length of the plate.

Distribution.—Fiji.

Types.—Holotype male, allotype female,



Figs. 1–13. Figs. 1–7, *Downeshelea stenochora*, 1–5, female; 6–7, male; Figs. 8–13, *Monohelea beaveri*, 8–11, female; 12–13, male: 1, 11, femora and tibiae of (left to right) fore, mid and hind legs; 2, hind tarsus; 3, 9, antenna; 4,8, palpus; 5, 10, spermathecae; 6, 12, parameres; 7, 13, genitalia, parameres omitted.

Viti Levu, Savura Creek, Colo-i-Suva, Fiji, iv.1983, R. A. Beaver, in Malaise trap. Paratype, 1 male, same data except v.1983.

Etymology.—The specific name is from the Greek: *stenos*—narrow, and *chora*—space, referring to the unusually narrow radial cells of this species.

Discussion.—Six species of *Downeshelea*

are known from the Australasian Region (Wirth and Grogan 1988): *leei* (Debenham 1972) from New South Wales, *medanieli* (Tokunaga, in Tokunaga and Murachi 1959) from the Caroline Islands, *nigra* (Tokunaga 1963) from New Guinea, *sepikensis* (Debenham 1972) from New Guinea, *unimaculata* (Debenham 1972) from New South Wales, and *xanthogonna* (Tokunaga 1963) from New Guinea. Of these species, *D. stenochora* most closely resembles *xanthogonna,* with the same general structure of the male genitalia, especially the setae on the ninth sternum, shape of the apicolateal processes on the ninth tergum, and the general plan of the aedeagus and parameres. However, *D. xanthogonna* is readily distinguished from *stenochora* by its more restricted wing pattern, the shorter and broader radial cells, and the different shapes of the aedeagus and the distal portions of the parameres.

Genus *Echinohelea* Macfie

Reference: Debenham, 1970: 145 (revision, species of Australia and New Guinea; key).

Echinohelea flava Tokunaga

Echinohelea flava Tokunaga, 1963: 235 (female; New Britain; figs.); Debenham, 1970: 151 (descriptive notes; male described and figured is not *flava*; New Guinea, Solomon Is.).

Recorded Distribution.—New Britain, New Guinea, Solomon Islands.

New Records.—FIJI: Viti Levu, Lami, ii.1981 (Krauss), 6 males, 7 females (BISH); Naussori Highlands, 500–700 m, xi.1976 (Krauss), 1 male, 1 female; Navai, 10.ii.1971 (Krauss), 1 male; Colo-i-Suva, Savura Creek, v.1983 (Beaver), 1 male.

Genus *Monohelea* Kieffer

References: Tokunaga and Murachi, 1959 (Micronesian species); Tokunaga, 1959, 1963 (New Guinea species); Debenham, 1972 (revision Australia and New Guinea species); Ratanaworabhan and Wirth, 1972 (revision Oriental species); Clastrier, 1985a (New Caledonia species); Wirth and Grogan, 1988 (diagnosis of genus and check list of species for world).

Remarks.—Wirth and Grogan (1988) divided the traditionally recognized genus *Monohelea* into three genera, *Monohelea* Kieffer, *Allohelea* Kieffer, and *Downeshelea* Wirth and Grogan, for which they gave diagnoses and world lists of species. They restricted the genus *Monohelea* to two groups, the *tigrina* group, an Australasian group of clear-winged species, and the *hieroglyphica* group, a large and widespread group with a hieroglyphic type wing pattern and extensively banded legs. They listed 10 species of the *hieroglyphica* group from the Australasian Region; species of this grouyp are difficult to separate except for details of the male genitalia. Adults of both sexes of the species occurring in Fiji, however, can be separated by the following key:

Key to the Fijian Species of *Monohelea*

1. Hind femur pale except for subapical dark band . . . 2
– Hind femur dark at least on proximal half . . . 3
2. Mid femur and tibia pale except apex of tibia . . . . . *coloisuvae* new species
– Mid femur and tibia brownish . . . . . *fijiensis* new species
3. Second radial cell of wing without infuscated area; costa short, costal ratio 0.79; hind femur brown on proximal 0.75, pale on distal 0.25; fore and mid femora and tibiae pale brown except broadly pale at knees . *beaveri* new species
– Second radial cell with large infuscated area; costa long, costal ratio 0.89; hind femur brown except for two distal oblique narrow pale rings; fore and mid femora pale with subapical dark band, tibiae pale with subbasal dark band and apical dark band . . . . . *leveri* new species

Monohelea beaveri Wirth and Giles, New Species
Figs. 8–13, 52

Female allotype.—Wing length 0.76 mm; breadth 0.30 mm.

Head: Yellowish, antennae pale brown, palpi whitish. Eyes broadly separated, bare.

Antenna (Fig. 9) with lengths of flagellar segments in proportion of 11-9-10-10-10-11-11-12-13-13-14-15-20; antennal ratio 0.90. Palpus (Fig. 8) with lengths of segments in proportion of 3-4-6-5-11; third segment with small round sensory pit. Mandible with eight small teeth.

Thorax: Pale brown; mesonotum with dark brown mottling seen in slide-mounted specimen; scutellum yellow. Legs (Fig. 11) pale yellowish with pale brownish bands as follows: proximal 0.6 of femora, all except bases of fore and mid tibiae, and a moderately broad subbasal band and distal fifth of hind tibia; bands on hind legs more intense. Hind leg with lengths from femur to tarsomere 5 as 114-103-50-24-16-18-13; hind basitarsus with abrupt bend near base and with row of palisade setae; tarsi without prominent ventral spines. Claws nearly straight, subequal on fore and mid legs, a single long claw on hind leg; lengths 0.043 mm on fore leg, 0.040 mm on mid leg, and 0.058 mm on hind leg. Wing (Fig. 52) with pattern typical of *hieroglyphica* species group; no dark spot in midportion of second radial cell; costal ratio 0.79; radial cells well formed, first 0.55 as long as second. Halter whitish with end of knob brown.

Abdomen: Pale brown. Spermathecae (Fig. 10) two; greatly unequal in size and shape, the larger 0.062 mm by 0.046 mm including neck, ovoid with short thick neck; the smaller subspherical, 0.026 mm by 0.023 mm, without neck but with long, threadlike sclerotization of the duct.

Male holotype.—Wing length 0.70 mm; breadth 0.30 mm.

Similar to the female with the usual sexual differences. Wing slightly narrower; costa shorter, costal ratio 0.70. Antenna with sparse brownish plume; segments 6–12 fused; antennal ratio 0.67. Legs with markings as in female; hind leg with lengths from femur to tarsomere 5 as 95-86-48-34-16-10-12; claws short, equal and similar on all legs, very slender and pointed and nearly straight.

Genitalia (Fig. 13): Dark brown; short, about as broad as long. Basistyle stout and tapering; dististyle nearly as long as basistyle, slender and curving gradually to tip. Aedeagus typical of *hieroglyphica* group, the well-sclerotized, triangular, lateral sclerites joined basally by a sclerotized loop, the median dorsal membrane with bilobed caudal margin, the lobes sharp-pointed. Parameres (Fig. 12) with the winglike anterior lobes joined mesally by a narrow sclerotized bridge, the caudal portions well separated, each a slender, nearly straight column slightly expanded distally, especially in lateral view, and abruptly recurved on distal portion in a slender pointed process bent ventrally.

Distribution.—Fiji.

Types.—Holotype male, allotype female, Viti Levu, Colo-i-Suva, Savura Creek, v.1983, R. A. Beaver, Malaise trap. Paratypes, 9 males, 9 females, as follows: VITI LEVU: Same data as types, 4 males, 6 females; same but iv.1983, 4 males, 3 females. Naraiyama, 178°5′E, 17°56′S, 18–30.xi.1986, R. L. Brown, UV light trap, 1 male.

Discussion.—This species is dedicated with pleasure to R. A. Beaver of the Biology Department, University of the South Pacific in Suva, in appreciation of his kindness and assistance to the senior author during his visit to Fiji in 1985.

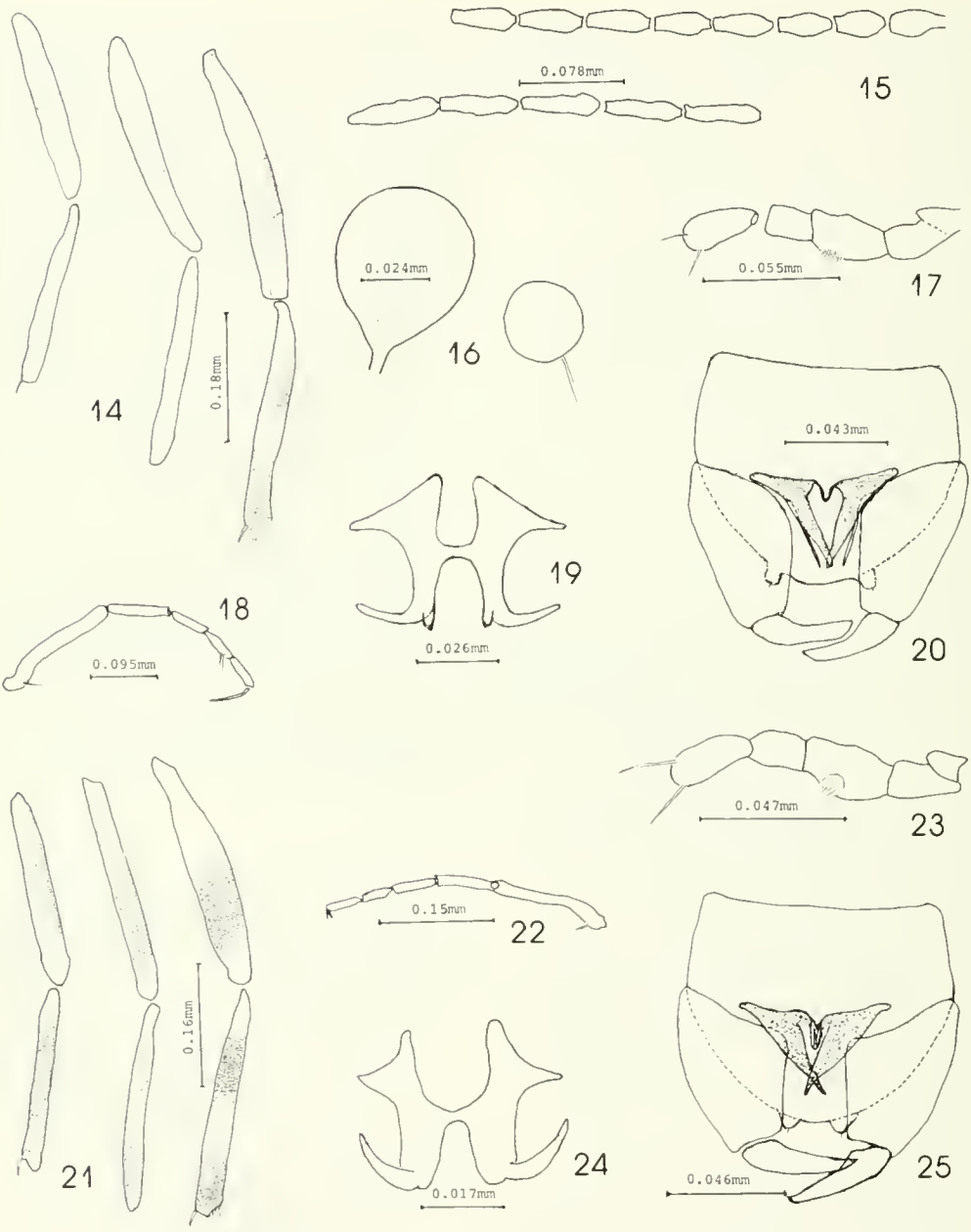
Monohelea beaveri can be distinguished from the three other Fijian species of *Monohelea* by the characters presented in the key above.

Monohelea coloisuvae Wirth and Giles, New Species

Figs. 14–20, 53

Female allotype.—Wing length 0.78 mm; breadth 0.33 mm.

Head: Yellowish, antenna pale brown, palpi whitish. Eyes broadly separated, bare. Antenna (Fig. 15) with lengths of flagellar segments in proportion of 12-10-12-13-14-14-14-15-16-17-17-17-20; antennal ratio



Figs. 14–25. Figs. 14–20, *Monohelea coloisuvae*, 14–18, female; 19–20, male; Figs. 21–25, *M. fijiensis*, male; 14, 21, femora and tibiae of (left to right) fore, mid and hind legs; 15, antenna; 16, spermathecae; 17, 23, palpus; 18, 22, hind tarsus; 19, 24, parameres; 20, 25, genitalia, parameres omitted.

0.83. Palpus (Fig. 17) with lengths of segments in proportion of 4-5-8-6-8; third segment with inconspicuous small round sensory pit. Mandible with eight small teeth.

Thorax: Yellowish with brownish mottling; scutellum yellow. Legs (Fig. 14) pale yellowish, coxae brownish. Hind leg with three brown bands; femur with an oblique

band just past midlength continued as a narrow infuscation ventrally to tip of femur; tibia with narrow brown band just before midlength and a broad brown area covering distal fourth. Hind leg with lengths from femur to tarsomere 5 as 115-100-50-25-16-13-13. Claws long and slender, slightly curving, subequal on fore and mid legs, a single long claw on hind leg (Fig. 18); lengths 0.044 mm on fore leg, 0.039 mm on mid leg, and 0.064 mm on hind leg. Very slender ventral spines on tarsi as follows: One subbasally on mid and hind basitarsi; a pair at apices of fourth tarsomeres, and a pair at apices of tarsomeres 1–3 on mid leg. Wing (Fig. 53) with hieroglyphic pattern as in *M. beaveri*; CR 0.79. Halter whitish with end of knob brown.

Abdomen: Pale brownish. Spermathecae (Fig. 16) two, greatly unequal in size and shape; the larger 0.067 by 0.049 mm including neck, ovoid, tapering to slender neck, with faint perforations in sclerotization on tapering portion near neck; the smaller 0.029 mm in diameter, spherical, without neck but with long, threadlike sclerotization of the duct.

Male holotype.—Wing length 0.72 mm; breadth 0.30 mm.

Similar to the female with the usual sexual differences; costal ratio 0.74. Antenna with sparse brownish plume; segments 6–12 fused; distal three segments elongated, antennal ratio 0.90. Legs with markings as in female, femora slightly infuscated on fore and mid legs, ventral infuscation at tip of hind femur fainter; hind leg with lengths from femur to tarsomere 5 as 97-90-47-24-14-11-12; claws short, equal and similar on all legs, very slender and pointed, and nearly straight.

Genitalia (Fig. 20): Brown, about as broad as long. Ninth tergum convex distally with small, moderately separated, papilla-like apicolateral processes. Dististyle short, half as long as basistyle, moderately stout and tapering to blunt-pointed tip. Aedeagus with lateral sclerites rather slender distally, each flanked by a slender hyaline blade subequal in length. Parameres (Fig. 19) joined in a narrow bridge near midportions, bases expanded winglike as usual in *hieroglyphica* group; distal portions each moderately slender and gradually tapering to ventrolaterally directed distal process, a small rounded ventromesal lobe at the base of the bent distal process.

Distribution.—Fiji.

Types.—Holotype male, Viti Levu, Naraiyama, 28–30.xi.1986, R. L. Brown, UV light trap. Allotype female, Viti Levu, Coloi-Suva, Savura Creek, v.1983, R. A. Beaver, Malaise trap. Paratypes, 2 females, same data as allotype; 2 males, 3 females, same data but iv.1983.

Discussion.—The species takes its name from the locality near Suva on Viti Levu where the allotype and paratypes were collected. *Monohelea coloisuvae* can be distinguished from the three other Fijian species of *Monohelea* by the characters presented in the key above. It is the Fijian species with the most restricted brownish leg markings, and the shapes of the distal portions of the parameres are diagnostic.

Monohelea fijiensis Wirth and Giles, New Species

Figs. 21–25, 54

Male holotype.—Closely resembling the preceding species, *Monohelea beaveri*, but differing as follows: Wing length 0.69 mm; breadth 0.27.

Head: Antenna with lengths of flagellar segments in proportion of 20-7-7-7-7-7-6-5-5-6-20-20-23, antennal ratio 0.82. Palpus (Fig. 23) with lengths of segments in proportion of 6-9-17-10-16, third segment with small round sensory pit.

Thorax: More extensively brownish, but scutellum almost entirely yellowish. Legs (Fig. 21) pale brownish, knees narrowly pale; hind femur and tibia pale with three broad dark bands, one subapically on femur, second sub-basally on tibia, and third at apex of tibia. Hing leg with lengths from femur

to tarsomere 5 as 92-80-453-23-15-12-12. Claws small, equal and simple on all legs (Fig. 22). Wing (Fig. 54) with dark markings as in *beaveri*, but not quite as extensive; costal ratio 0.67.

Genitalia (Fig. 25): Shorter and broader than in *beaveri*; ninth tergum more convex distally, apicolateral processes smaller and rounded and set closer together near midline. Dististyle short and tapering, only two-thirds as long as basistyle. Aedeagus with lateral sclerites stouter, the basal loop not well developed. Parameres (Fig. 24) short and stout, joined in midportion at about half their length; each distal portion a broad, distally rounded plate, from the apex of which arises a moderately slender, tapering process of about the same length, curving ventrolaterad.

Distribution.—Fiji.

Types.—Holotype male, one male paratype, Viti Levu, Colo-i-Suva, Savura Creek, iv.1983, R. A. Beaver, Malaise trap. One male paratype, Naraiyama, Viti Levu, 28–30.xi.1986, R. L. Brown, UV light trap.

Discussion.—*Monohelea fijiensis* can be separated from its three Fijian congeners by the characters given in the key above.

Monohelea leveri Wirth and Giles, New Species
Figs. 33–39, 55

Female allotype.—Wing length 0.70 mm; breadth 0.36 mm.

Head: Pale brown, antennae darker, palpi paler. Eyes broadly separated, bare. Antenna (Fig. 36) with lengths of flagellar segments in proportion of 10-7-7-8-8-9-10-10-12-12-13-15-20; antennal ratio 1.04. Palpus (Fig. 35) short and stubby; lengths of segments in proportion of 3-4-6-5-8; sensory pit on third segment small and round. Mandible with eight strong teeth.

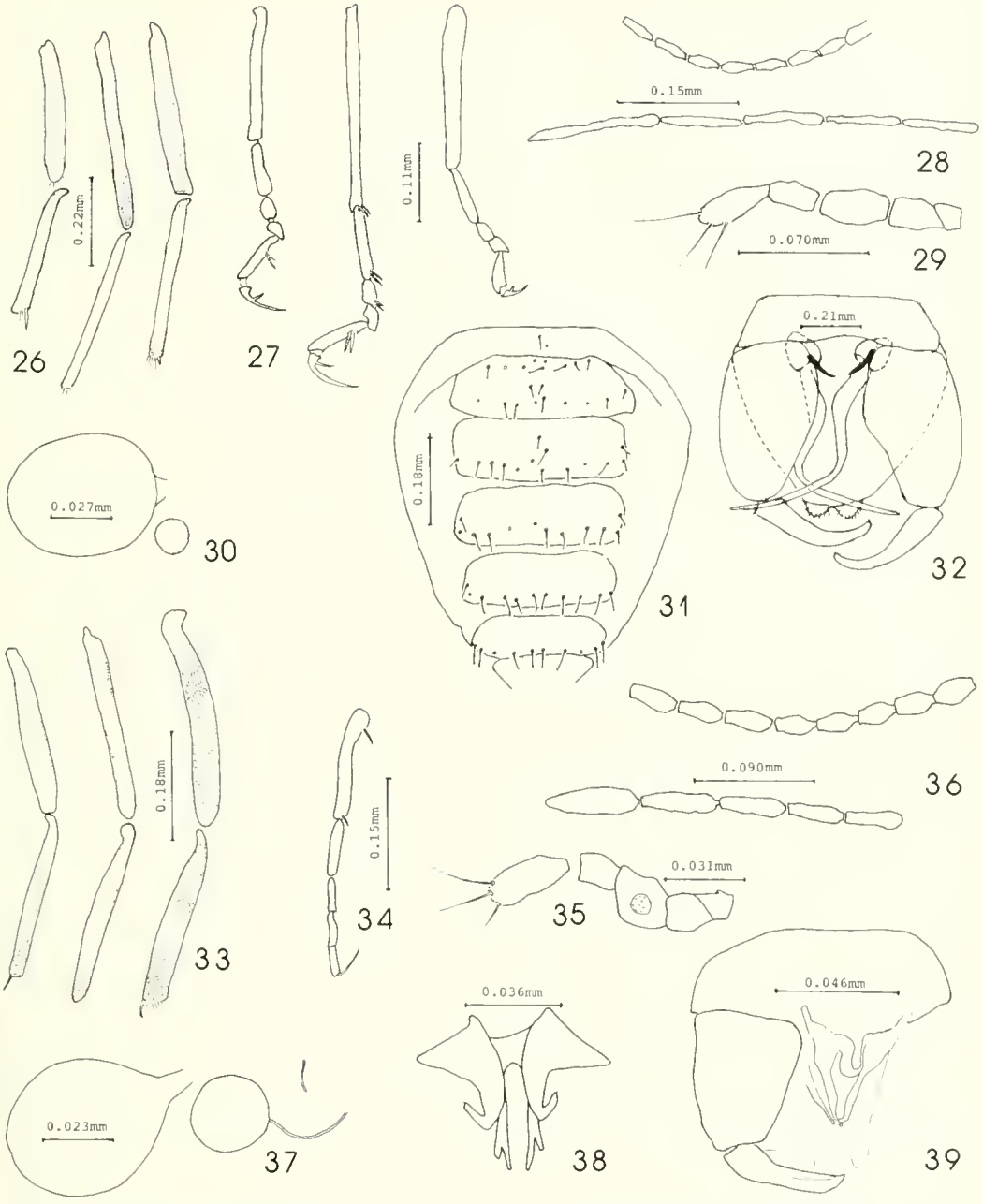
Thorax: Brown including scutellum. Legs (Fig. 33) brown; distal third of fore femur and proximal third of fore tibia pale, also a broad but incomplete subapical pale band on fore tibia; mid femur pale on mid third, mid tibia pale on mid half; hind femur and tibia dark brown except narrow pale bands in midportion. Hind leg with lengths from femur to tarsomere 5 as 96-82-43-20-13-12-12; hind femur and tibia slightly thickened and hind femur slightly bowed. Mid and hind basitarsi with a strong spine near base and a pair of slender spines at apex (Fig. 34); a pair of slender spines at apices of tarsomeres 2–4 on mid leg. Claws nearly straight, subequal on fore and mid legs, a single long claw on hind leg; lengths 0.029 mm on fore leg, 0.026 mm on mid leg, and 0.046 mm on hind leg. Wing (Fig. 55) with dark hieroglyphic pattern much more extensive than in other Fijian species, a prominent dark mark included in midportion of second radial cell; costa unusually long, costal ratio 0.89. Halter brown.

Abdomen: Pale brown. Spermathecae (Fig. 37) two, greatly unequal in size and shape, the larger 0.069 by 0.046 mm including neck, ovoid with short thick neck; the smaller spherical, 0.029 mm in diameter, without neck but with long, threadlike sclerotization of the duct.

Male holotype.—Wing length 0.67 mm; breadth 0.27 mm.

Similar to the female with the usual sexual differences; wing narrower and costa shorter as normal in the genus; costal ratio 0.80. Antenna with sparse, pale brownish plume, segments 6–12 fused as usual; antennal ratio 0.77. Legs with markings as in female; hind leg with lengths from femur to tarsomere 5 as 94-80-42-22-15-12-13; claws short, equal and similar on all legs, very slender and pointed and nearly straight.

Genitalia (Fig. 39): Slightly broader than long, brownish. Ninth tergum covex distad, with short, papilla-like apicolateral processes. Dististyle stout and tapering to blunt point, about two-thirds as long as basistyle. Aedeagus with darkly sclerotized basal loop, the lateral sclerites slender distally, flanked laterally by a slender process similar to that of *M. coloisuvae*. Parameres (Fig. 38) short and broad, the lateral wings at base well



Figs. 26–39. Figs. 26–32, *Stilobezzia browni*, 26–31, female; 32, male; Figs. 33–39, *Monohelea leveri*, 33–37, female; 38–39, male: 26, 33, femora and tibiae of (left to right) fore, mid and hind legs; 28, 36, antenna; 29, 35, palpus; 30, 37, spermathecae; 31, abdominal terga; 32, genitalia; 38, parameres; 39, genitalia, parameres omitted.

developed; main stem portion of each unusually short, tapering and abruptly bending ventrolaterally in a hooklike process; the stem portion continuing straight caudally in a prominent, rather slender, unequally forked, distal process twice as long as the hooklike ventrolateral process.

Distribution.—Fiji.

Types.—Holotype male, allotype female, Viti Levu, Colo-i-Suva, Savura Creek, iv.1983, R. A. Beaver, Malaise trap.

Discussion.—The species is dedicated to the memory of R. J. A. W. Lever, for many years the Government Entomologist for the British Colony of Fiji, and the foremost authority on the economic insects of the southwestern Pacific islands. The insect collection at the Agriculture Station at Koronivia remains a well-curated collection of specimens, the great majority of which were collected by Lever.

Monohelea leveri differs markedly from the three other known species of Fijian *Monohelea*, distinguished by its stout legs, more brownish color with more extensively dark wing markings, more extensive brownish leg markings, and especially by the unusually long costa and second radial cell. The male parameres, with their short, curved, lateral process and long, straight, unequally-forked, distal process, are diagnostic. *Monohelea palauensis* Tokunaga (in Tokunaga and Murachi 1959), a widespread Pacific species, is closely related, with stout legs, wing pattern with a dark mark in the second radial cell, and male genitalia of a similar structure, but *palauensis* differs in its shorter costa (female costal ratio 0.79), paler legs, and different proportions on the distal processes of the male parameres.

Genus *Stilobezzia* Kieffer

References: Lee, 1948: 345 (key to Australia and New Zealand species); Tokunaga and Murachi, 1959: 363 (Micronesian species); Tokunaga, 1963: 249 (key to New Guinea species); Das Gupta and Wirth, 1968: 1 (revision of Oriental species; generic diagnosis).

Stilobezzia bifurcata Tokunaga

Stilobezzia bifurcata Tokunaga, 1959: 307 (male, female; New Guinea; figs.); Tokunaga, 1963: 271 (notes; New Guinea records); Debenham, 1978: 472 (Australasian literature and distribution).

Recorded distribution.—Irian Jaya, New Britain, New Guinea.

New records.—FIJI: Viti Levu, Ovalau, Levuka, xi.1975, N. L. H. Krauss, 1 female (BISH); Korotongo, iii.1981 (Krauss), 1 male (BISH); Lami, ii.1981 (Krauss), 1 male; same, i,iii.1971, iii.1976, ii.1977, xii.1978 (Krauss), 1 male, 7 females; 14 km w Lami, 7–10.xii.1986, R. L. & B. B. Brown, UV light trap, 2 males, 4 females.

Stilobezzia (*Stilobezzia*) *browni* Wirth and Giles, New Species

Figs. 26–32, 56

Allotype female.—Wing length 1.05 mm; breadth 0.36 mm.

Head: Yellowish brown; palpi and antennal flagellum, except bases of first eight segments, dusky. Eyes contiguous, bare. Antenna (Fig. 28) with lengths of flagellar segments in proportion of 16-13-13-13-13-14-14-14-30-30-30-30-40; antennal ratio 1.46. Palpus (Fig. 29) with lengths of segments in proportion of 5-7-12-10-12. Mandible with seven coarse teeth.

Thorax: Pale brownish. Legs (Fig. 26) yellowish, hind leg with lengths from femur to tarsomere 5 as 120-110-60-22-7-6-16; without strong setae except a few at tips of femora. Hind basitarsus with 2½ rows of palisade setae; one row on first two tarsomeres of fore and mid legs and tarsomere 2 of hind leg; fourth tarsomere of fore and mid legs with pair of strong black batonnets. A single long claw on each leg, claw with slender basal tooth nearly half as long as claw; length of claw 0.058 mm on fore leg, 0.080 mm on mid leg and 0.038 mm on

hind leg (Fig. 27). Wing (Fig. 56) pale grayish hyaline, without macrotricnia, veins slightly infuscated; first radial cell small, slightly elongate; second radial cell spacious; costal ratio 0.68. Halter brownish.

Abdomen: Yellowish; terga brownish, with setae arranged in pattern as figured (Fig. 31). Spermathecae (Fig. 30) two, greatly unequal in size and shape; the larger brownish, 0.072 by 0.058 mm, oval without sclerotized neck; the smaller hyaline, spherical, 0.017 mm in diameter.

Holotype male.—Wing length 1.05 mm; breadth 0.33 mm.

Similar to the female with the usual sexual differences. Eyes broadly separated, bare. Antenna with well-developed plume which is yellowish proximally, dusky distally; lengths of flagellar segments in proportion of 25-14-14-14-14-14-14-14-14-16-43-50-72; antennal ratio 1.08. Palpus as in female. Thorax darker brown than in female, scutellum paler. Legs yellowish, distal third of mid femur slightly darkened; tarsomeres 1–3 of mid leg with pair of distal spines ventrally; fifth tarsomeres without batonnets; claws short, equal, distally cleft on all legs. Wing as in female but narrower; costal ratio 0.66. Halter with dark brown knob.

Genitalia (Fig. 32): Pale brownish, broader than long; ninth tergum convex caudally with a submedian pair of prominent setose cerci. Basistyle short, stout, tapering distally; dististyle half as long as basistyle, curved, gradually tapered to slender pointed tip. Aedeagus reduced to a pair of small linear sclerites extending obliquely caudomesad from base of basistyle. Parameres separate, each with prominent basal knob, main portion in form of a very elongate, strongly sclerotized, sickle-like blade slightly swollen on proximal third, straighter on distal half.

Distribution.—Fiji.

Types.—Holotype male, allotype female, Viti Levu, 14 km w Lami, 7–10.xii.1986, R. L. and B. B. Brown, UV light trap. Paratypes, 1 male, 1 female, same data; 1 male, Suva, Koronivia Agr. Sta., 6.xii.1968, S. Singh, light trap (BISH).

Discussion.—This species is named for Richard L. Brown in appreciation of his interest and cooperation in making available to us his fine collection of ceratopogonids taken during his visit to Fiji in 1986.

Stilobezzia browni belongs to the *subviridis* group of the subgenus *Stilobezzia* as characterized by Das Gupta and Wirth (1968), but is not closely related to any of the Oriental species described in that group. It is most similar, especially in the shape of the male parameres, to *S. flavizonata* Tokunaga (1963), described from New Guinea, but that species (male only) is paler yellow, the abdomen dark with two basal terga pale yellow, and the aedeagus shaped differently.

Tribe Heteromyiini
Genus *Clinohelea* Kieffer

Reference: Debenham, 1974: 6 (revision, species of Australia and New Guinea; key).

Clinohelea tasmaniensis Lee

Clinohelea tasmaniensis Lee, 1948: 65 (male, female; Tasmania; figs.); Debenham, 1974: 7 (redescribed; Australia records).

Recorded distribution.—Australia (Tasmania to southern Queensland).

New records.—FIJI: Viti Levu, Lami, iii.1955, iii.1976, N. L. H. Krauss, 2 females; Nagali, xi.1957 (Krauss) (BISH), 1 female; Suva, Koronivia, 6.xii.1968 (Singh), light trap, 1 female (BISH).

Note.—The two Fiji females agree well with an Australian female in the USNM, except that the fore femur is dark brown only at the extreme tip in Fiji specimens.

Tribe Sphaeromiini
Genus *Hebetula* Wirth and Debenham

Reference: Debenham, 1974: 22 (revision Australia and New Guinea spp.; as *Mixohelea*); Wirth and Debenham, 1977: 282 (diagnosis; list of included species).

Hebetula tonnoiri (Lee)

Xenohelea tonnoiri Lee, 1948: 66 (female; Tasmania; figs.); Tokunaga, 1966: 116 (female redescribed; New Guinea).

Mixohelea tonnoiri (Lee); Debenham, 1974: 22 (combination; male, pupa described; Australia records; figs.).

Hebetula tonnoiri (Lee); Wirth and Debenham, 1977: 282 (combination).

Recorded distribution.—Australia, New Guinea.

New records.—FIJI: Ovalua, Levuka, iii.1969 (Krauss), 1 female (BISH). Viti Levu, Lami, i,iii.1971, iii.1976, ii.1977, xii.1978 (Krauss), 12 females (BISH). 2 km N Naraiyawa, 27.x.1986, R. L. Brown, at light, 1 male, 1 female (USNM); Nausori Highlands, 500--700 m, 26.iii.1970 (Krauss), 1 female (BISH); Suva, Koronivia Agr. Sta., 6.xii.1968 (Singh), light trap, 1 female (BISH); Suva, xi.1957 (Krauss), 2 females (BISH); Tholo-i-Suva, i.1955 (Krauss), 1 female (USNM).

Genus *Nilobezzia* Kieffer

Reference: Debenham, 1974: 62 (revision species Australia and New Guinea); Wirth and Ratanaworabhan, 1981: 408 (key to Oriental species).

Nilobezzia fijiensis
Wirth and Giles, New Species
Figs. 40–44, 57

Holotype female.—Wing length 2.48 mm, breadth 0.74 mm.

Head: Dark brown including antenna and palpus. Eyes broadly contiguous. Antenna (Fig. 40) with lengths of flagellar segments in proportion of 25-13-13-13-13-13-14-16-42-42-40-40-50, antennal ratio 1.65. Palpus (Fig. 41) with lengths of segments in proportion of 10-15-20-8-12; second segment broadest, succeeding segments progressively more slender. Mandibles with five and seven teeth.

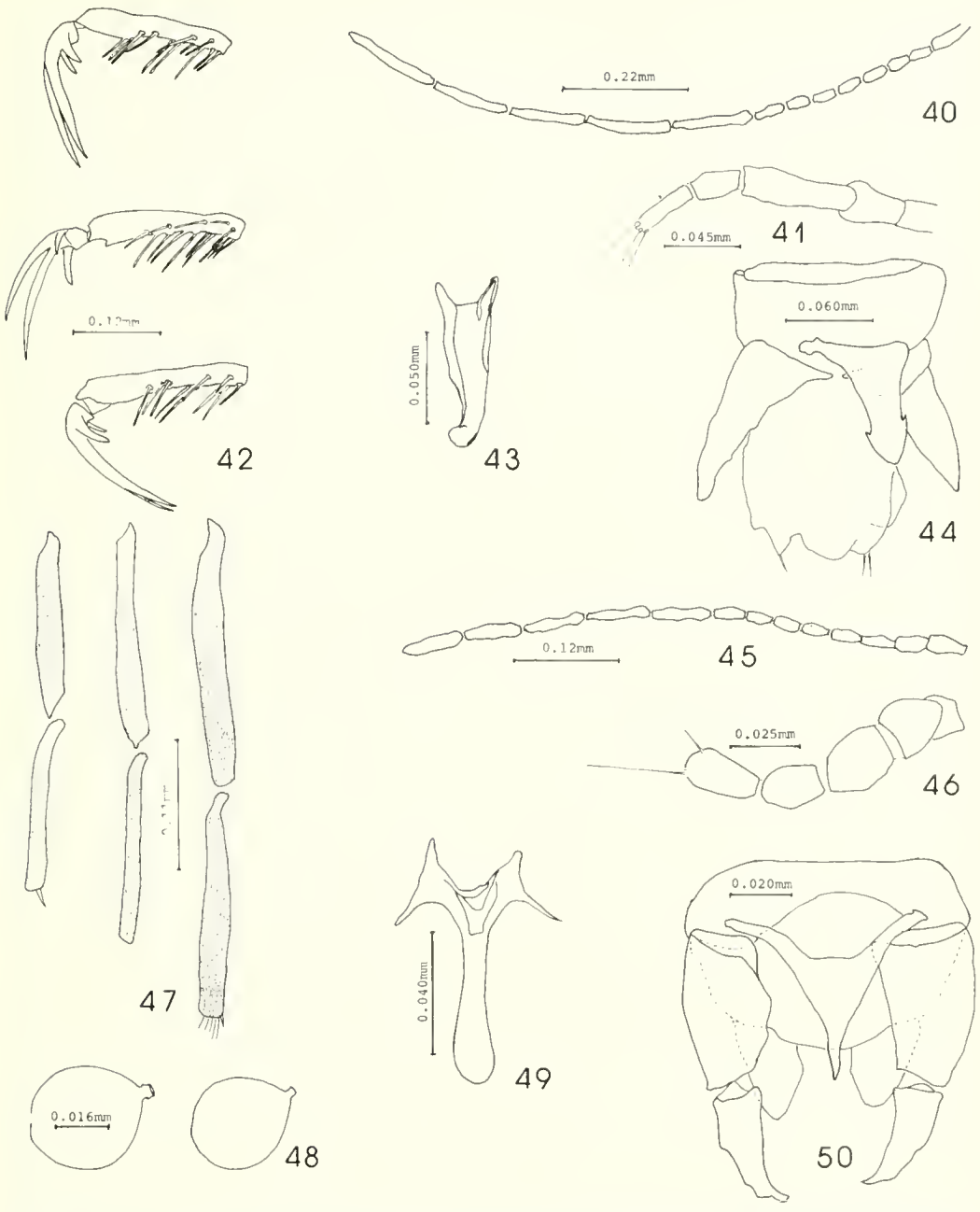
Thorax: Dark brown including scutellum (pinned paratype was mounted from fluid and thorax is dirty, pollinosity obscured if present). Legs dark brown; tarsi yellowish but narrow apices of tarsomeres 1, 3, most of 4, and all of tarsomere 5 brownish. Femora each with one strong black ventral spine at apex; tibiae with 5–6 enlarged bristles scattered along dorsal side; tarsomere 5 (Fig. 42) with 12 black batonnets on fore leg, 14 on mid leg, and 10 on hind leg; claws 0.9 as long as fifth tarsomeres, external tooth 0.27 as long as claws. Wing (Fig. 57) pale smoky grayish, anterior veins yellowish; costal ratio 0.84. Halter brown.

Abdomen: Dark brown. Gonopore flanked by several short bristles and 4–5 long black bristles on each side. Spermathecae obscured on slide mount; shapes and measurements not discernible.

Allotype male.—Taken at a different time and place, the specimen described here is the presumed male of *N. fijiensis,* in spite of minor differences in setation and the paler color presumed to be due to prolonged storage in alcohol.

Wing length 1.47 mm; breadth 0.45 mm; costal ratio 0.72. Thorax dark brown, head and legs paler brownish; wing grayish, radial veins slightly infuscated; halter brownish. Eyes contiguous. Antenna with sparse pale brownish plume; lengths of flagellar segments in proportion of 28-16-15-15-15-16-16-16-17-24-28-28-x; last segment not in position to measure. Palpus stubby; lengths of segments in proportion of 3-7-12-5-8. Legs without strong spines at apices of femora.

Genitalia (Fig. 44): Dark brown; shape and structure typical of the genus, with short ninth sternum and elongate ninth tergum with irregularly convex posterior margin. Basistyle and dististyle inperceptibly fused in a long, irregularly tapering lobe three-fourths as long as tergum. Aedeagus a triangular sclerite half again as long as basal breadth, with very slight anterior concavity, tapering distally to a slightly expanded cap-like tip. Parameres (Fig. 43) fused in another triangular tapering sclerite, slightly longer



Figs. 40–50. Figs. 40–44, *Nilobezzia fijiensis*, 40–42, female; 43–44, male; Figs. 45–50, *Bezzia vitilevuensis*, 45–48, female; 49, 50, male; 40, 45, antenna; 41, 46, palpus; 42, fifth tarsomere and claws of (top to bottom) fore, mid and hind legs; 43, 49, parameres; 44, 50, genitalia, parameres omitted; 47, femora and tibiae of (left to right), fore, mid and hind legs; 48, spermathecae.

and basally narrower than aedeagus, with slender knoblike tip bent posteroventrally.

Distribution.—Fiji.

Types.—Holotype female, Viti Levu, Lami, ii.1981, N. L. H. Krauss (USNM). Allotype male, Viti Levu, Suva, Koronivia Agr. Sta. 6.xii.1968, S. Singh, light trap (BISH). Paratype, 1 female, Viti Levu, Suva, iii.1956 (Krauss) (BISH).

Discussion.—*Nilobezzia fijiensis* closely resembles the widespread Oriental species *N. raphaelis* (Salm) in its uniformly dark brown femora and tibiae, dark brown antenna and abdomen, and femora with only 1–2 apical spines, but *raphaelis* differs in having pale palpi and whitish halteres. *Nilobezzia whartoni* Lee from Australia and New Guinea is similar but possesses pale halteres and a whitish abdomen.

Tribe Palpomyiini
Genus *Bezzia* Kieffer

References: Tokunaga, 1966: 141 (New Guinea species; key); Debenham, 1978: 557 (catalog, Australasian Region); Wirth and Ratanaworabhan, 1981: 413 (Southeast Asia species; key); Clastrier, 1985b: 45 (new species from New Caledonia).

Bezzia vitilevuensis
Wirth and Giles, New Species
Figs. 45–50, 58

Holotype female.—Wing length 1.02 mm; breadth 0.43 mm.

Head: Dark brown. Eyes broadly contiguous, bare. Vertex with strong spines curving over eyes. Antenna (Fig. 45) with lengths of flagellar segments in proportion of 15-12-12-11-10-10-10-10-20-20-20-20-21; antennal ratio 1.12. Palpus (Fig. 46) short and stubby; lengths of segments in proportion of 3-5-7-6-7. Mandible with nine coarse teeth.

Thorax: Dark brown; mesonotum with scattered erect spinelike setae; supra-alar setae especially long and spinelike. Legs (Fig. 47) dark brown, tarsi whitish; femora unarmed; tarsomeres 1 and 2 of mid leg with one row of palisade setae, 1 and 2 of hind leg with two rows of palisade setae. Hind leg with lengths from femur to tarsomere 5 as 124-106-70-26-13-10-15; claws short, curved, equal, each claw 0.032 mm long. Wing (Fig. 58) slightly brownish infuscated due to coarse dark microtrichia; radial veins brownish; wing especially broad; costal ratio 0.85. Halter dark brown, knob intensely brown.

Abdomen: Dark brown; one pair of gland rods extending anteriorly the length of two body segments. Spermathecae (Fig. 48) two, slightly ovoid with short narrow necks, slightly unequal, 0.039 by 0.032 mm and 0.036 by 0.029 mm including neck.

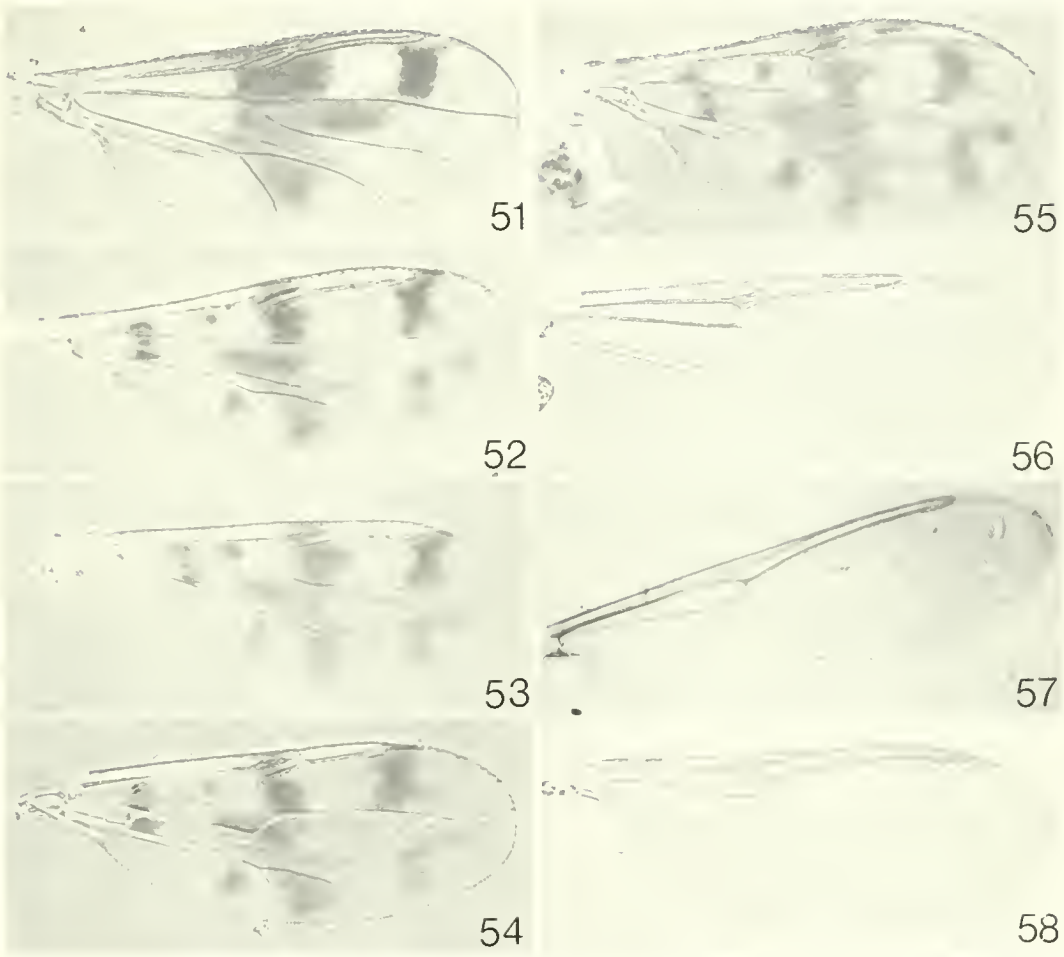
Allotype male.—Wing length 0.79 mm; breadth 0.32 mm; costal ratio 0.82.

Similar to the female with the usual sexual differences. Antennal plume very sparse and inconspicuous, pale brownish; flagellar segments with lengths in proportion of 20-10-10-9-8-8-8-9-10-13-22-22-25; antennal ratio 0.65. Palpus reduced to tiny globular segments; proportions 3-4-6-5-6. Hind leg with lengths from femur to tarsomere 5 as 106-94-52-23-13-7-13; palisade setae present only on tarsomeres 1 and 1 of hind leg, in two rows.

Genitalia (Fig. 50): Typical of the genus *Bezzia*; about as broad as long; ninth sternum short with shallow caudomedian excavation; ninth tergum short and convex, with long setose cerci. Basistyle short and tapering, without lobes; dististyle tapering irregularly to distal point. Aedeagus forming a nearly equilateral triangle; basal arms slender with low basal arch; distal process triangular, tapering to slender distal point. Parameres (Fig. 49) fused as usual in the genus; basal processes winglike with sharp anterior and lateral points; distal process long and spatuliform with slightly enlarged, rounded tip.

Distribution.—Fiji.

Types.—Holotype female, allotype male, Viti Levu, 14 km w Lami, 7–10.xii.1986, R. L. and B. B. Brown, UV light trap.



Figs. 51–58. Wings of Ceratopogonidae: 51, *Downeshelea stenochora*; 52, *Monohelea beaveri*; 53, *M. coloisuvae*; 54, *M. fijiensis*; 55, *M. leveri*; 56, *Stilobezzia browni*; 57, *Nilobezzia fijiensis*; 58, *Bezzia vitilevuensis*.

Discussion.—The specific name is from Viti Levu, the island where the species was taken. *Bezzia vitilevuensis* is readily distinguished from all other *Bezzia* species of the Oriental and Australasian Regions by the combination of uniformly dark brown femora and tibiae and lack of femoral armature.

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GONATOPUS BARTLETTI OLMI [HYMENOPTERA: DRYINIDAE] IN MÉXICO: A PREVIOUSLY UNREPORTED PARASITOID OF THE CORN LEAFHOPPER *DALBULUS MAIDIS* (DELONG & WOLCOTT) AND THE MEXICAN CORN LEAFHOPPER *DALBULUS ELIMATUS* (BALL) [HOMOPTERA: CICADELLIDAE]

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Abstract.—The dryinid *Gonatopus bartletti* Olmi was reared from parasitized *Dalbulus maidis* (DeLong & Wolcott) and *Dalbulus elimatus* (Ball) collected in México. This is the first record of this dryinid in México.

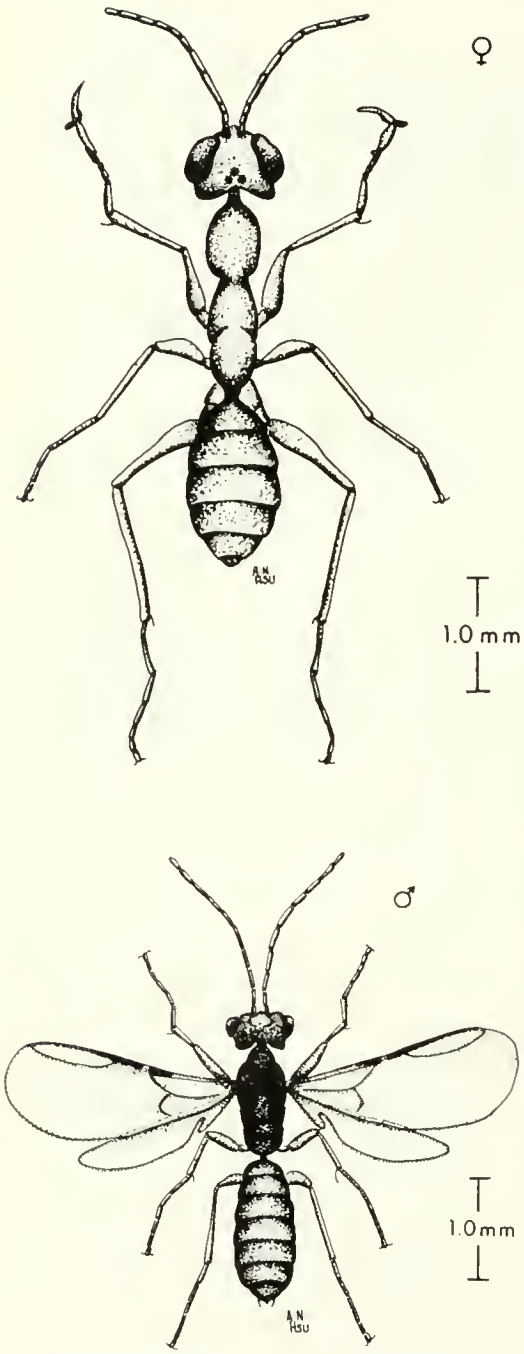
Key Words: corn leafhopper, *Dalbulus*, dryinids, *Gonatopus*, México

Although the corn leafhopper, *Dalbulus maidis*, is mainly found at low to mid elevations, and the "Mexican corn leafhopper," *Dalbulus elimatus*, is mainly found at high elevations (Barnes 1954, Nault in press), both species are pests of maize in México. These insects are capable of vectoring 3 maize stunting pathogens: maize rayado fino virus (MRFV), corn stunt spiroplasma (*Spiroplasma kunkelii* Whitcomb et al.), and maize bushy stunt mycoplasma-like organism (Nault 1985). Yield losses due to MRFV transmission by *Dalbulus maidis* have been estimated at 40–50% of the weight of a mature ear in maize cultivars adapted to Central America (Gámez and León 1985). In newly developed cultivars losses can reach 100% (Gámez and León 1985).

Little is known about natural enemies (Madden et al. 1986) or biological control of *Dalbulus* spp. In México, remnants of *Dalbulus* spp. were found in webs of the spider *Tetragnatha* sp. (Araneae: Tetragnathidae). Feeding by this spider on *Dalbulus* was confirmed in the laboratory (F. E. Vega, unpublished data). In the laboratory, *Hippodamia convergens* Guérin-Méneville nymphs and adults fed on adult *Dalbulus* (F. E. Vega, unpublished data). In Nicaragua, *Ectatomma ruidum* (Formicidae: Ponerinae) has been observed to prey on *Dalbulus maidis* (Perfecto 1989) while two fungi, *Metarhizium anisopliae* and *Beauveria bassiana*, are known to infect *Dalbulus maidis* (S. Gladstone, personal communication). So far, there is no information of *Dalbulus* egg predators or parasitoids.

Pipunculids, strepsipterans, and dryinids are known to attack leafhopper nymphs and adults (Waloff 1975), but in México, only dryinid parasitism has been observed (by F. E. Vega). In El Salvador, a dryinid identified as *Agonatopus* sp. was found attacking *D. maidis* (Quezada 1979), although it is suspected to be *Gonatopus bartletti* Olmi (M. Olmi, personal communication). *G. bartletti* was first reported from Puerto Rico (Bartlett 1939, Olmi 1984), but Olmi (personal communication) now has records from Nicaragua, Venezuela, Bahamas, and Belize. We present the first record of *G. bartletti* (Hymenoptera: Dryinidae) in México.

[1] Scientific article No. A-5033, contribution No. 8081 of the Maryland Agricultural Experiment Station.



Figs. 1–2. *Gonatopus bartletti* Olmi. 1. Female. 2. Male.

Materials and Methods

To identify the parasitoids attacking *D. maidis* and *D. elimatus,* leafhoppers were collected in maize fields in 6 Mexican states: Jalisco, Guanajuato, Querétaro, México, Morelos, and Veracruz. Although other plant hosts could have been sampled for *Dalbulus* spp. (e.g. *Tripsacum* and the teosintes), we presumed it most logical to begin a search in maize agroecosystems within the widest geographical area we could sample. Those insects showing symptoms of parasitism (e.g. a black spot in the abdomen or a bloated abdomen) were separated from the rest with a manual aspirator and taken to the laboratory where they were placed in plastic cups with plastic lids with a screen-covered rectangular hole. The cup contained about 1.5 cm of soil and fresh maize leaves which were replaced daily.

Results

Five specimens identified as *Gonatopus bartletti* Olmi (Dryinidae: Gonatopodinae) were reared: two apterous females from 2 parasitized *D. maidis* and one winged male and 2 apterous females from 3 parasitized *D. elimatus* (for a complete description of the Dryinidae, see Olmi 1984). Parasitized insects were collected at the Colegio de Postgraduados in Montecillos, state of México, and along Road 43, 19 km west of Celaya in the state of Guanajuato. Parasitism by dryinids was observed in the state of Jalisco in the Pacific coast and eastward to the state of Veracruz on the Gulf coast.

Only parasitoids in their late stages of development emerged, as indicated by the big sac on the host's abdomen (Waloff 1974). Before the parasitoid larva emerged, the leafhopper exhibited sluggish behavior, and its wings and elytron had been pushed upwards by the parasitoid sac. A few minutes before larval emergence the leafhopper clung to a leaf blade and died. After the parasitoid larva emerged, it moved around the cup, and spun a cocoon, either in the soil, in the leaf, or on the walls of the cup.

Table 1. *Dalbulus* species found in México.

D. quinquenotatus
D. chiapensis
D. maidis
D. tripsacoides
D. charlesi
D. gelbus
D. guzmani
D. longulus
D. guevarai
D. elimatus

Discussion

México is the putative center of origin for ten of eleven *Dalbulus* species (Table 1) (Nault and DeLong 1980, Triplehorn and Nault 1985). Due to the number of *Dalbulus* species, their host plants, and the habitats in which these can be found, it can be argued that there should be a wider diversity of natural enemies of *Dalbulus* in México than elsewhere. A search in maize plantations in six Mexican states revealed only *Gonatopus bartletti* Olmi. Although the importance of this dryinid as a biological control agent is not known, a study by Waloff (1974) suggests that dryinids have the potential to control leafhoppers. Using different leafhopper species she determined that a female *Gonatopus sepsoides* Westwood could potentially parasitize 177 leafhoppers over her lifetime.

Further research on rearing methods, and the bionomics of this dryinid will determine the feasibility of the use of *Gonatopus bartletti* Olmi as a biological control agent. An extended search for natural enemies of all other *Dalbulus* species may uncover other parasitoids and predators which might act against *Dalbulus maidis* and *Dalbulus elimatus*.

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92(3), 1990, pp. 465–470

A NEW HOST RECORD FOR *EURYTOMOCHARIS ERAGROSTIDIS* HOWARD (CHALCIDOIDEA:EURYTOMIDAE) INFESTING *ERAGROSTIS TEF* IN SOUTH DAKOTA

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Abstract.—The species *Eurytomocharis eragrostidis* is for the first time recorded from South Dakota infesting *Eragrostis tef* grown in the Americas. The female ovipositor, propodeum and male reproductive apparatus are illustrated.

Key Words: Hymenoptera, Eurytomidae, *Eurytomocharis eragrostidis* Teff, South Dakota

Stem-boring Hymenoptera infest cereal crops and numerous other grasses (Essig 1958). The genus *Eurytomocharis* was found to infest up to 30% of stems of several range grasses in New Mexico (Watts and Bellotti 1967). Bugbee (1966) redefined the genus *Eurytomocharis* and described 4 new species from stems of grasses.

Teff [*Eragrostis tef* (Zucc.) Trotter] is the primary grain crop of Ethiopia. This crop is currently being evaluated as a potential new forage crop for the northern Great Plains (Boe et al. 1986). Stunted growth of the crop in South Dakota in 1988 prompted dissection of stems that revealed larvae of *Eurytomocharis eragrostidis* Howard feeding inside. The observations and data reported here describe a new insect-plant relationship and the magnitude of infestation of teff by *E. eragrostidis* at 2 widely-separated South Dakota locations. Anatomical descriptions, illustrations of male and female genitalia and additional morphological structures are presented to assist in the identification of *E. eragrostidis*.

Materials and Methods

In late July 1988, 7 random teff plants from each of 4 replications in field trials at Brookings and Highmore, South Dakota, were examined for infestation by *E. eragrostidis*. The trials were planted on 17 May and 1 June 1988 at Highmore and Brookings, respectively.

Tillers of each plant were slit longitudinally with a razor blade and numbers of larvae, pupae, and exit holes were determined for each mature internode. Approximately 30 internodes containing larvae or pupae were placed in small, covered glass jars and adults that emerged in the summer and fall of 1988 were collected for identification.

Results and Discussion

Plant–insect interaction.—*E. eragrostidis* infested a high percentage of teff tillers at both South Dakota locations in 1988. Individual tillers frequently had more than one infested internode, resulting in 28 and 38% internode infestation at Brookings and Highmore, respectively (Table 1).

Watts and Bellotti (1967) reported that the 4 *Eurytomocharis* species found infesting range grasses in the southwestern United States had similar life cycles with only 1 generation per year on any given grass species. In South Dakota, exit holes were

Table 1. Infestation rates of teff by *Eurytomocharis eragrostidis* at two South Dakota locations in 1988.

Location	Numbers examined		Percent infested[1]	
	Tillers	Internodes	Tillers	Internodes
Highmore	132	449	72 ± 12	38 ± 4
Brookings	158	434	50 ± 7	28 ± 3

[1] Mean ± standard deviation of 4 replications.

found in approximately 30% of the infested teff internodes in late July (Fig. 1) and adults of *E. eragrostidis* emerged under laboratory conditions in August and September 1988. More research is needed to determine if a second generation can be produced on teff in South Dakota.

Teff had been grown at both locations for more than 5 years with no previous indication of stem-boring insect problems. *E. eragrostidis* has been previously reported from *Agropyron* spp., *Agrostis alba* L., *Andropogon saccharoides* Swartz, *Eragrostis cilianensis* (All.) Lutati., *E. erosa* Scribn., *E. poaeoides* Beauv. ex Roem. and Schult., *Muhlenbergia porteri* Scribn., *M. wrightii* Vasey, *Oryzopsis hymenoides* (Roem. and Schult.) Ricker, and *Sporobolus airoides* (Torr.) Torr. (Burks 1979).

Watts and Bellotti (1967) found *E. eragrostidis* most frequently on side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.] in New Mexico. *E. cilianensis* and side-oats grama occur commonly throughout South Dakota, but more study is needed to determine if these species are hosts of *E. eragrostidis* in the northern Great Plains.

Several parasitic chalcids have been frequently recorded from stem-boring eurytomids in range grasses (Watts and Bellotti 1967). No parasitic chalcids emerged from teff internodes stored in the laboratory nor were any observed in dissected stems. However, since dissection frequently destroyed the enclosed larvae, few adults were reared from the samples. Exit holes observed in plants in the field in July may have been made by parasites of *E. eragrostidis*. A more thorough study would be required to determine if *E. eragrostidis* is parasitized in teff.

Fig. 1. Exit hole of *Eurytomocharis eragrostidis* in teff.

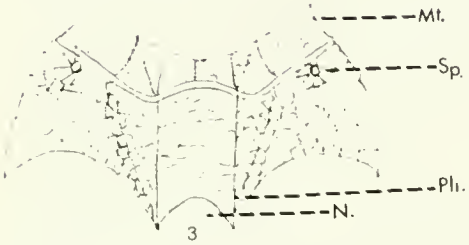
The apparent reduction in growth due to *E. eragrostidis* may be an important factor influencing the potential of teff for forage production in the northern Great Plains. Forage yields of teff at both locations in 1988 were approximately one-fourth of the forage yields obtained for several years prior to the discovery of infestation by *E. eragrostidis* in 1988. Watts and Bellotti (1967) observed similar stunting symptons in range grasses from which they collected *E. eragrostidis*.

External and reproductive structure morphology.—The following description is based on 19 specimens collected from teff, of which 2 females and 2 males were sent to the United States National Museum for identification.

Female: Head dark black; mesosoma black to reddish black; pronotum, propodeum, petiole, gastor bluish black; antenna with scape yellow (two specimens had dark scape); flagellum yellow, bordered with brown; maxillary palp white; mandibles white; legs with coxae, trochanters, femora and tibia yellow; tarsi yellow; gena carinate,

head with fairly deep piliferous punctures dorsally between ocelli extending past posterogenal region; plesosoma with same piliferous punctures; head with frons concave between eyes; antennal scrobes at base of concave frons at or below eye; scape longer than pedicel and first funicular segment together; funicular segments separated by short stalk; club segments fused, 3 in number, first two similar in shape and size to funicular segments, last segment broad at base, narrowing to rounded apex; mesosoma collar broad, edge rounded, without punctures; pronotum with piliferous punctures; scutellum convex, scutoscutellar sulcus continuous, both covered with piliferous punctures; marginal vein broader and longer than postmarginal; parastigma with clear region at attachment to marginal; stigmal subequal to postmarginal, shorter than marginal; submarginal vein with single sensillum behind first dorsal submarginal setae; dorsal parastigma with 2 sensilla, pigmented portion extending anterior of sensilla, the remainder clear with light pigmentation in center; costal cell with single row of dorsal setae, ventral surface with scattered setae; speculum closed; cubital hair line and medial hair line distinct; propodeum (Fig. 3) with light yellow tinge, lighter than scutellum, darker than hind coxae, area near coxae setose, plated, center with shallow furrow, asetose, all plates irregular in shape not punctured as found on scutellum (Fig. 3); Ovipositor (Fig. 2) semicircular sheaths (2nd valvifers) with 2 setae near laminated bridge, rami spines not fixed in number (mean numbers of spines were 36.6 ± 2.1 and 36.8 ± 1.6 for left and right rami of a sample of 6 females); fulcral plate and inner ovipositor plate attached to semicircular sheets; fulcral plate notched with four monitoring spines; attachment of outer ovipositor plate is in-between fulcral plate notch and attachment of fulcral plate and curved ramus edge; outer ovipositor plate fused with eighth tergite; eighth tergite contains button-like cercus with five setae of different sizes and shapes; near cercus a series of setae are found to be dispersed along the eighth tergite, (these are more numerous near the cercus becoming single toward the fulcral plate); eighth tergite setal region plated, bordered by dark line that divides fused outer ovipositor plate into different pigmented areas; apex of eighth tergite with series of long setae; inner ovipositor plate separated from semicircular sheath by darkened region; below darkened region is a groove in which the fulcral plate fits along with monitoring spines; inner ovipositor plate plated to region of fused ovipositor sheath; ovipositor sheath not articulated; ovipositor sheaths lightly plated with longitudial striae with a series of setae at apex.

Male: Color similar to female with head dark black; mesosoma, pronotum, propodeum black; petiole elongated, black; gastor black; ventor dark due to dark coxae in some specimens, other specimens with coxae yellow similar to female; antennae with scape darker than in female; flagellum lighter than body color, with five funicular segments, long setae and well-developed petiole segments; maxillary palp and mandibles yellow; legs with coxae dark, similar in color to body, with some yellow; trochanters, femora and tibia yellow, hind femora with some brown in middle section; tarsi yellow; sculpturing similar to female; wings same as female except medial not distinguished by a single row of setae, rather with 2–3 closely set setae marking region of medial hairline; costal cell same as female; basal setae well-developed, joining cubital hairline closing speculum; male reproductive apparatus (Figs. 4, 5) with aedeagus bilobed, each lobe with 6 sensory pores on ventor; parameres with 2 setae, one associated with apex which is usually hidden between the digiti and the aedeagus, second setae on the narrow arm of the fused parameres, the latter larger than apical setae; single ventral setae located on expanded portion of parameres; digiti with 2 spines, digiti with paired pore-like structures and paired digital apodemes; aedeagal apodemes protrude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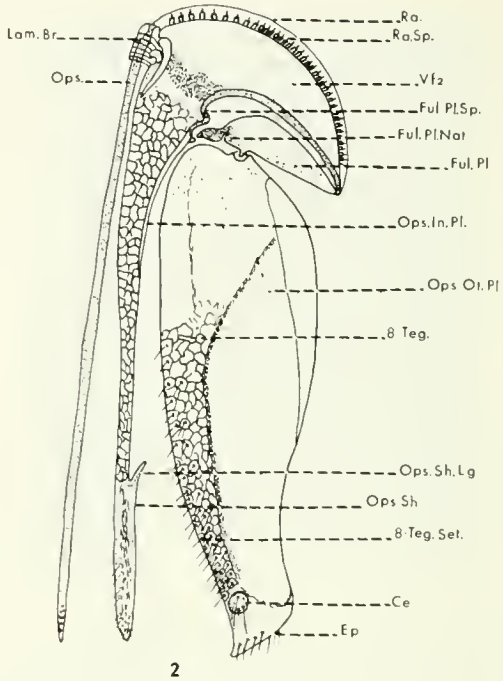
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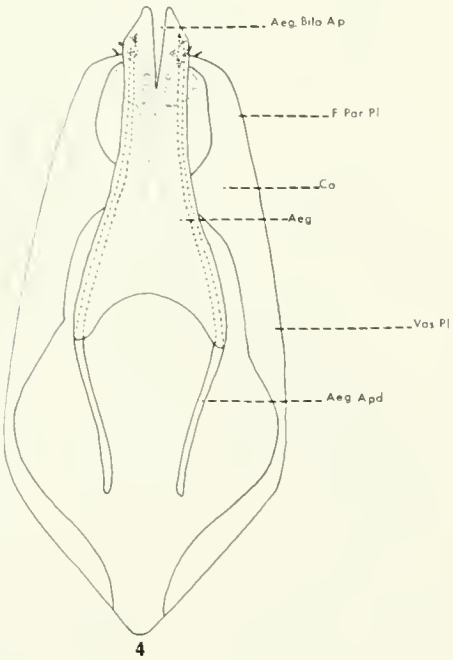
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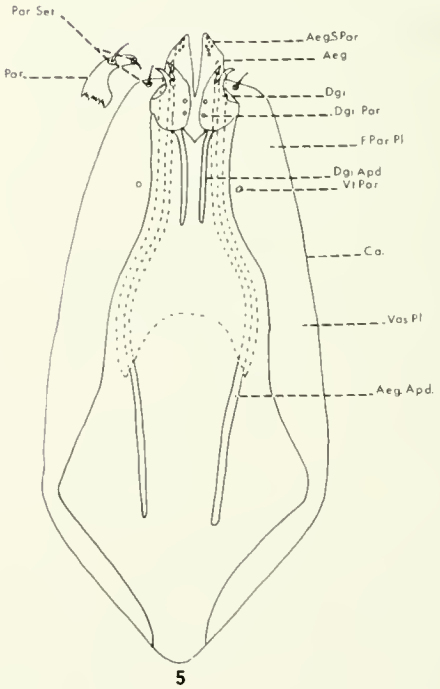
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from caulis; aedeagus dorsally covers digiti and caulis; a covering attached to the eighth tergite is torn away from aedeagus when removing whole male reproductive structure (this structure is covered with small setae and may function in insertion of the aedeagus into the female). At apex of aedeagus on dorsal surface are pigmented raised areas (these raised areas are not the same pigmented pores that are observed on the aedeagus of members of the genus *Bruchophagus*).

Copland and King (1972) stated that the number of rami spines varies with species but did not indicate that they vary within individual females as well as between valvifers of a single female. In *E. eragrostidis* reared from teff the mean number of ramus spines was 36.7. The numbers of left and right ramus spines were equal in only two of the six females examined. The largest difference found between number of left and right ramus spines within an individual female was four (39 on the left ramus and 35 on the right ramus). Rami spines are considered to be sensory in nature, serving to monitor the position of the stylets (Copland and King 1972). They are most widely spaced in the region close to the laminated bridge becoming closer together near attachment of fulcral plate. In a current study of the genus *Bruchophagus*, we have found that the mean number of ramus spines can be used to statistically separate the closely related species that attack leguminous seeds.

Arrangement of eighth tergite setae has been found to be of value in separating closely related species of the genus *Bruchophagus* and may well be a diagnostic structure in separating species of *Eurytomocharis*. However, we have not examined other species of *Eurytomocharis* to determine if setal arrangment differences do exist within the genus.

In *E. eragrostidis* the ovipositor sheaths are connected by a ligament. This ligament is easily torn during slide preparation, giving the appearance that the ovipositor sheaths are not connected. On slide-mounted genitalia the ovipositor sheaths have a lip-like projection that is the broken ovipositor sheath ligament. It is from these projections that the thin ligament is attached connecting the ovipositor sheaths.

Acknowledgments

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Fig. 2. Ovipositor of *Eurytomocharis eragrostidis* collected from teff in South Dakota. Abbreviations: (Lam. Br.) Laminated bridge; (Ra) Ramus; (Ra. Sp.) Ramus Spines; (Vf2) 2nd valvifer (Semicircular sheath); (Ful. Pl.) Fulcral plate (1st valvifer); (Ful. Pl. Not.) Fulcral plate notch; (Ful. Pl. Sp.) Fulcral plate spines; (Ops. In. Pl.) Ovipositor Inner Plate (3rd valvulae); (Ops. Ot. Pl.) Outer ovipositor plate (8th tergite); (Ops.) Ovipositor (1st & 2nd valvulae); (Ops. Sh.) Ovipositor sheath; (Ops. Sh. Lg.) Ovipositor Sheath Ligament; (Ce.) Cercus; (8-Teg. Set.) 8th tergite setae; (Ep.) Epipygium; (8-teg.) 8th tergite.

Fig. 3. Female propodeum. Abbreviations: (Mt.) Metanotum; (Sp.) Spiracle; (Pli.) Plica; (N.) Nucha (neck).

Figs. 4, 5. Male reproductive apparatus, dorsal, and ventral respectively. Abbreviations: (Aeg. S. Por.) Aedeagal sensory pores; (Aeg.) Aedeagus; (Dgi.) Digiti; (Dgi. Por.) Digiti pore; (F. Par. Pl.) Fused Paramere Plate; (Dgi. Apd.) Digiti apodemes; (Vt. Por.) Ventral Pore; (Ca.) Caulis; (Vos. Pl.) Volsellar Plate; (Aeg. Apd.) Aedeagus apodemes; (Aeg. Bilo. Ap.) Aedeagus Bilobed apex.

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THE *NEMOMYDAS* OF SOUTHWESTERN UNITED STATES, MEXICO, AND CENTRAL AMERICA (DIPTERA: MYDIDAE)

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Abstract.—The species of *Nemomydas* Curran occurring in the southwestern United States, Mexico, and Central America are reviewed. Thirteen species are recognized, including two new species, **N. fronki** n. sp. and **N. wendyae** n. sp. The males of *N. brachyrhynchus* (Osten Sacken) and *N. sponsor* (Osten Sacken) are described for the first time, *N. fumosus* Hardy is elevated to a full species, and *N. panamensis* (Curran) is considered a *nomen dubium*. A key to the males is provided.

Key Words: *Nemomydas* key, new species

Nemomydas Curran is a distinctive genus of mydas flies found in North and Central America, and contains a number of geographically restricted species. Hardy (1950) revised the North American species, and Steyskal (1956) reviewed the species in the eastern United States. However, our knowledge of the Mexican and Central American species is poor. Recent collections from Mexico, Guatemala, southwestern United States, as well as the examination of type specimens, has made it possible to review the fauna of this area and clarify the taxonomic status of several regional species.

Papavero and Wilcox (1968) transferred *Mydas senilis* Westwood to *Nemomydas*. Our examination of the male holotype of this species indicate it as a true *Mydas* as defined by Wilcox and Papavero (1971), and a member of the *interruptus* group (Welch and Kondratieff 1990). We also examined the types of *N. desideratus* (Johnson) (MCZ #7592) and *N. jonesii* (Johnson) (MCZ #7593) as well as available specimens of *N. lara* Steyskal and *N. melanopogon* Steyskal. These four species are restricted to the southeastern United States, especially Florida. *Nemomydas lara*, originally described from females, is probably the female of *N. melanopogon*, a species known only from males.

Specimens for this study were provided by the following institutions: British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Canadian National Collection (CNC); Colorado State University (CSU); Florida State Collection of Arthropods (FSCA); Michigan State University (MSU); Museum National D'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard (MCZ); San Diego Natural History Museum (SDNHM); University of Arizona (UA); University of California, Berkeley (UCB); University of Colorado (UC); University of Kansas (UK); and the United States National Museum of Natural History (USNM).

Methods of preparation, and terminology of the male genitalia, follow Wilcox and Papavero (1971) and Wilcox (1981). This study illustrates, for the first time, the male terminalia of all species known from this region. The females of *N. bifidus* Hardy, *N. solitarius* (Johnson), and *N. tenuipes* (Loew)

are unknown, therefore no key is presented for the females. We follow Snelling's (1987) political designations for Lower California.

Key to the Males of *Nemomydas* of Western North America and Central America

1. Aedeagus in lateral view, enlarged or expanded (Figs. 2–5) 2
– Distal section of aedeagus tube-like and elongate in lateral view (Figs. 1, 6–13) 6
2. Distal section of aedeagus abruptly expanded and recurved medially in lateral view (Figs. 2, 4) 3
– Aedeagus swollen, tapering apically in lateral view (Figs. 1, 3, 5) 4
3. Abdominal tergites yellowish brown (in some specimens, tergites shaded with brownish black); terminalia as Fig. 2. Distribution: southwestern United States (Arizona) and northern Mexico (Sonora) ..... *brachyrhynchus* (Osten Sacken)
– Abdominal tergites black with posterior margins of tergites 2–6 yellow; terminalia as Fig. 4. Distribution: Guatemala and Costa Rica ..... *sponsor* (Osten Sacken)
4. Abdominal tergites black, posterior margins of 1–6 or 1–7 yellow 5
– Abdominal tergites yellow brown with middorsal blackish brown spots or dashes; terminalia as Fig. 1. Distribution: Honduras ..... *bequaerti* (Johnson)
5. Aedeagus in lateral view tongue-like, constricted medially (Fig. 3). Distribution: Costa Rica ..... *lamia* (Séguy)
– Aedeagus in lateral view broad basally, tapering apically with small flange anteroapically (Fig. 5). Distribution: Mexico ..... *wendyae* n. sp.
6. Tergites entirely black or reddish black 7
– Tergites reddish, yellow, yellowish brown or dark and distinctly marked with white or yellow 8
7. Dorsal digitate process of gonocoxite in lateral view, small originating from inner surface of ventral digitate process (Fig. 6); body and legs entirely black, covered by long black setae. Distribution: Texas ..... *fronki* n. sp.
– Dorsal digitate process of gonocoxite in lateral view, large originating at base of ventral digitate process (Fig. 7); thorax, tergite 1 or 2 with yellow or white setae. Distribution: California, Mexico (Baja California) ..... *tenuipes* (Loew)
8. Tergites brownish black or black marked with yellow or white 9
– Tergites reddish yellow, yellow or yellowish brown 10
9. Tergites 1–7 black or brownish black with transverse yellow margins posteriorly; basal portions of hind femur and tibia yellow; terminalia as in Fig. 13 ..... *venosus* (Loew)
– Tergites brownish black, tergites 3–5 with triangular, whitish spots laterally; basal portions of hind femur and tibia blackish brown; terminalia as Fig. 11 ..... *fumosus* Hardy
10. Dorsal digitate process of gonocoxite, in lateral view, small, originating from inner surface of ventral digitate process (Fig. 12). Distribution: Colorado ..... *solitarius* (Johnson)
– Dorsal digitate process of gonocoxite, in lateral view, originating at base of ventral digitate process (Figs. 8, 9). Distribution: British Columbia south to Mexico (Baja California) 11
11. Proboscis short, 0.8–0.9 times as long as subcranial cavity ..... *pantherinus* (Gerstaecker)
– Proboscis long, 1.3 times as long as subcranial cavity 12
12. Abdominal tergites and legs with dense yellow to white setae ..... *intonsus* Hardy
– Abdominal tergites and legs with black setae ..... *bifidus* Hardy

Nemomydas bequaerti (Johnson)
Figs. 1, 14

Leptomydas bequaerti Johnson, 1926: 144. Type locality: Honduras, Depto. Colon, Puerto Castilla. Holotype male (MCZ #7594), examined.

Nemomydas bequaerti, Papavero and Wilcox, 1968: 34.10.

Johnson (1926) provided an adequate description of both sexes of this species. In his key, Johnson stated that *N. bequaerti* has cell r_5 open; however, our examination of all material available, including the holotype male, showed that this cell is closed. The following may be added to the original description of the male: proboscis short, 0.6 times as long as subcranial cavity; tergite 1 with long erect whitish setae; and tergites 2–7 with recumbent, short, black setae.

The extent of the middorsal blackish brown dashes or spots on abdominal tergites is variable. The holotype and 1 additional specimen have these marks on ter-

gites 2–7, whereas another specimen has these marks only on tergites 2–3.

Nemomydas bequaerti may be easily separated from all others in this study (Central American *Nemomydas*) by the short stubby aedeagus (Fig. 1), and tergites 2–7 yellow-brown with middorsal blackish brown dashes or spots. The female of *N. bequaerti* is very similar to the female of *N. brachyrhynchus* Osten Sacken, but may be distinguished by the more elongate second flagellomere (Fig. 14), and apparent geographical distribution (Honduras). The female of *N. brachyrhynchus* has an expanded second flagellomere (Fig. 15) and is known from northern Mexico (Sonora) to southern Arizona.

Material examined.—HONDURAS: Holotype male as noted above; paratype male, same data except 28 III 1924 (MCZ); Puerto Castilla, 2 IV 1926, R. H. Painter, 2 males, 1 female (CAS); same data 1 male, 1 female (CNC); same data but 26 III 1924, 1 male, 1 female (BMNH).

Nemomydas brachyrhynchus (Osten Sacken)

Figs. 2, 15

Leptomidas brachyrhynchus Osten Sacken, 1886: 69. Type locality: (Northern) Sonora, Mexico. Holotype female (BMNH), examined.

Leptomydas brachyrhynchus, Johnson, 1926: 142.

Nemomydas brachyrhynchus, Hardy, 1950: 25.

Nemomydas brachyrhynchus, Papavero and Wilcox, 1968: 34.10.

Male.—Length 12–19 mm. Head shiny black, setae erect, golden yellow to white; antenna 3.2 mm long, reddish black, tinted with orange, especially apically; proboscis short, 0.8 times long as subcranial cavity, reddish brown. Scutum reddish brown to reddish black, 3 broad brownish black stripes slightly converging posteriorly; scutellum shiny brown; posterior portion of postnotum blackish brown; wing hyaline, membrane around longitudinal veins tinted with brown; halter yellow; legs yellowish brown, except coxa and trochanters shiny brown, distal portion of hind femur and tibia brownish black, tarsus tinted with brown, setae on distal portion of hind femur and hind tibia black, others yellow. Abdominal tergites usually yellowish brown, in some specimens shaded with brownish black, pleural margins blackish brown; bulla black, setae long, erect and whitish to yellow on tergite 1, short, recumbent and black on tergites 2–7; sternites yellowish brown, darker posteriorly.

Terminalia.—Yellowish-brown, gonocoxite tinted with blackish-brown; dorsal digitate process of gonocoxite slender, curving inward; aedeagus in lateral view, apically expanded (Fig. 2).

This is the first description of the male. Hardy (1950) suggested that *N. brachyrhynchus* was a possible synonym of *N. pantherinus*. The association of the male with the female clearly indicates that this species is distinct. Males of *N. brachyrhynchus* can be easily distinguished from all other *Nemomydas* by the combination of aedeagus with an enlarged apical section, (Fig. 2) and usually with yellowish brown abdomen. Several specimens from Sonora, Mexico, and Arizona have tergites shaded with brownish black. The aedeagus of *N. sponsor* (Fig. 4) is similar to that of *N. brachyrhynchus* but the male of *N. sponsor* has a black abdomen with yellow posterior margins on tergites 2–6. The female of *N. brachyrhynchus* is similar to the females of *N. bequaerti*, *N. pantherinus* (Gerstaecker) and the light phase of *N. venosus* (Loew). However, *N. brachyrhynchus* is readily distinguished from *N. pantherinus* by the following features: (1) lacking long dense postocular setae (*N. pantherinus* has long dense postocular setae); (2) lacking dense lateral scutal setal fringe (*N. pantherinus* has a dense fringe of long yellow to white setae); and (3) abdominal tergites without brown transverse bands

(*N. pantherinus* females have brown anterior transverse bands on tergites 2–5). The light phase of *N. venosus* also lacks the dense, long postocular setae, and the dense lateral scutal setal fringe, but has abdominal tergites 2–4 or 2–7 with brown anterior transverse bands. Characters for separation of the female of *N. brachyrhynchus* from *N. bequaerti* are given in the discussion of the latter species.

Material examined.—MEXICO: Sonora, holotype female (BMNH); 7 mi. S. Alamos, Rio Cuchajachi, 20 March 1985, L. Stange and R. Miller, 2 males (FSCA); ARIZONA: Cochise Co., 2 mi. NE of Portal, 30 V 1962, J. Wilcox, 1 female (CAS); Pima Co., Madrona Ranger. Sta., W. Rincon Mts., 15 V 1964, at mud and water, M.L. Noller, J. C. Bequaert, H. Eltom, M. Nurein, F. G. Werner, 1 female (UA); Sabino Canyon, 26 V 1962, F. D. Parker and L. A. Stange, 2 males (CAS); same data except 8 V 1961, Sharp, 1 male; Santa Catalina Mtns., 9 V 1950, J. Markley, 1 female (UA); same data except 30 IV 1955, F. G. Werner, 1 female (CAS); same data except 30 IV 1955, F. G. Werner, 1 male (UA); same data except 1 V 1956, G. D. Butler, 1 male (UA); same data except 13 V 1960, Halberg, 1 female (UA); same data except 5 V 1961, B. Bryce, 1 male (UA); same data except 8 V 1961, R. Band, 1 male (UA); same data except Wargo, 1 male (UA); same data except 8 V 1961, C. Jackson, 1 female (UA); same data except 11 V 1962, Huiscir, 1 female (UA); same data except 13–14 V 1962, E. Stout, 1 male, 1 female (UA); same data except 6 V 1966, B. L. O., 1 female (UA); same data except 6 V 1966, G. Roux, 1 male (UA); same data except 9 V 1966, Donald, 1 male (UA); same data except Molino Basin, 12 V 1980, C. Olson, MacLachlan, 1 male (UA); Tucson, 21 IV 1957, Witman, 1 female (UA); same data except 6 V 1962, D. Parks, 1 male (UA); Santa Cruz Co., Madera Canyon, 17–21 V 1971, J. Wilcox, 2 males, 2 females (CAS); Bear Canyon, 12 V 1961, E. M. Painter, 1 male (CAS); Santa Rita Mtns., VIII 1977, C. A. Olson, 1 female (UA).

Nemomydas lamia (Séguy)
Fig. 3

Nomoneura lamia Séguy, 1928: 146. Type locality: La Caja, Costa Rica. Lectotype male (here designated and so labelled, MNHN), examined.

Nemomydas lamia, Papavero and Wilcox, 1968: 34.11.

Male.—Length 13 mm. Head shiny black, setae erect, whitish; orbital margin of compound eye whitish; antenna 3.2 mm long, brown, tinted reddish brown and gray pollinose apically; proboscis long, 2.3 times as long as subcranial cavity, black. Scutum black, with pair of submedian yellowish pollinose stripes converging posteriorly, a pair of lateral yellowish pollinose stripes, setae whitish, sparse, erect; postnotum with lateral yellowish white areas; wings hyaline, longitudinal veins brown; halter brown; foreleg and midleg brown, setae whitish, hindleg brown with basal portion of femur yellowish, setae whitish dorsally, black ventrally on femur, spines reddish brown; tibia brown. Abdominal tergites shiny black, posterior margins on tergites 1–7 yellow, bulla black, setae long and erect, whitish on tergites 1–2, short and whitish on 3–7; sternites shiny black, setae long, whitish and erect.

Terminalia.—Reddish-brown; ventral digitate process of gonocoxite thickened, thumb-like; dorsal digitate process slender, curved inward; aedeagus in lateral view tongue-shaped, constricted medially; in ventral view tapering apically (Fig. 3).

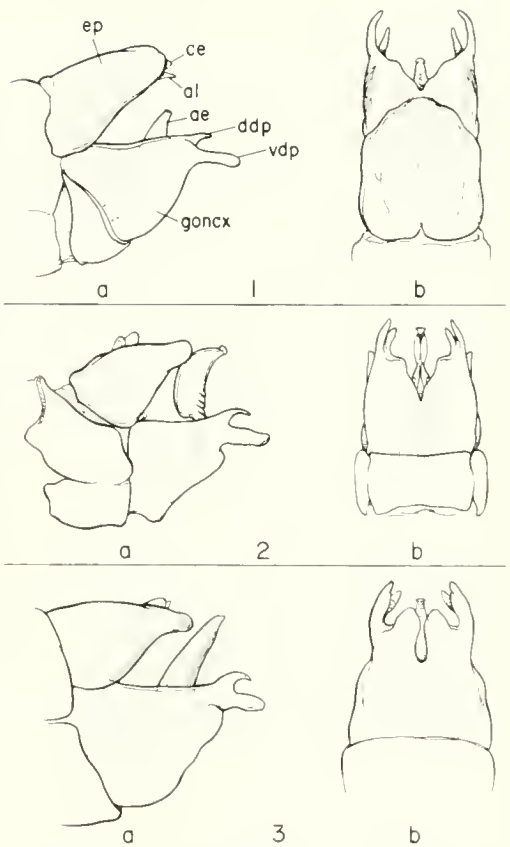
Female.—Length 15–18 mm. General coloration and structure similar to males except posterior margins on tergites 1–4 or 5 yellow.

Material examined.—COSTA RICA: La Caja, Paul Serre, 1920, Lectotype male designated (marked with blue margined lecto-

type label); 6 female paralectotypes, same label data as lectotype (MNHN).

Remarks.—Séguy (1928) did not designate a holotype. The syntypes of *N. lamia* sent to us by D. Baylac (Museum National D'Histoire Naturelle) consisted of a male marked with a red type label and a label "*Nemoneura lamia* Seguy, type," (considered here as the lectotype), a female marked also as "type," another male and 6 females. These 8 specimens have similar Costa Rica locality labels and determination labels of N. Papavero (in 1970). The second male syntype is identical to the male of *N. sponsor* and included under that species. The 6 females are all considered to be *N. lamia*. The male of *N. lamia* can be distinguished from the closely related *N. wendyae* and *N. sponsor* by the distinctive aedeagus (Fig. 3) and the whitish setae of the head.

The females of *N. lamia*, *N. sponsor*, and *N. wendyae* are very similar. *Nemomydas lamia* has blackish brown abdominal tergites, with tergites 1–4 or 5 with yellow posterior transverse margins. Both *N. sponsor* and *N. wendyae* have tergites 5–7 reddish brown.



Figs. 1–3. 1. *Nemomydas bequaerti*. Male terminalia, a. lateral, b. ventral. Abbrev.: ae, aedeagus; al, anal lamellae, ce, cercus; ddp, dorsal digitate process; ep, epandrium; goncx, gonocoxite; vdp, ventral digitate process. 2. *Nemomydas brachyrhynchus*. Male terminalia, a. lateral, b. ventral. 3. *Nemomydas lamia*. Male terminalia, a. lateral, b. ventral.

Nemomydas sponsor (Osten Sacken)

Fig. 4

Leptomydas sponsor Osten Sacken, 1886: 68. Type locality: San Geronimo, Guatemala. Holotype female (BMNH), examined.

Male.—Length 14 mm. Head shiny black, setae erect, black to reddish brown; orbital margin of compound eye whitish; antenna 3.1 mm long, black, tinted with brown; proboscis long, 1.8 times as long as subcranial cavity, black. Scutum black, with pair of submedian gray white pollinose stripes converging posteriorly, a pair of lateral gray white pollinose stripes; anterior portion of scutellum gray white pollinose, posteriorly shiny black, setae whitish, sparse, erect; postnotum with lateral gray white areas; wings hyaline except membrane around longitudinal veins tinted with brown; halter black; foreleg and midleg black, setae yellowish, hindleg black with basal portion of femur yellowish, setae black ventrally on femur, spines reddish brown; tibia reddish black. Abdominal tergites shiny black, posterior margins of tergites 1–6 yellow, brown on tergite 8, bulla black, setae long and erect, whitish on tergites 1–2, short and black on 3–7; sternites shiny black, setae long, whitish and erect.

Terminalia.—Reddish brown, dorsal and ventral digitate processes of gonocoxite elongate; aedeagus constricted medially, expanded and recurved apically (Fig. 4).

Material examined.—COSTA RICA: 1 male (MNHN); GUATEMALA: Depto. Guatemala, Tacaton, Lago Amatitlan, near Villa Canales, 10 I 1989, B. C. Kondratieff, 1 male, 2 females (CSU); Holotype female, S. Geronimo, Champion (BMNH).

Remarks.—The male is described here for the first time. Osten Sacken (1886) presented an excellent descriptions of the female of this species. The male of *N. sponsor* resembles *N. lamia, N. wendyae* and *N. venosus* but may be immediately distinguished by the form of the aedeagus (Fig. 4).

The female is very similar to *N. wendyae* but can be separated by the distal flagellomeres being reddish brown and brown setae of face, whereas the female of *N. wendyae* has the antennae distally blackish-brown and white facial setae.

Nemomydas wendyae, New Species
Fig. 5

Male.—Length 13.5 mm. Head shiny black, setae erect, black; orbital margin of compound eye whitish; antennae 3.9 mm long, scape and pedicel black, flagellomere 1 and 2 brownish red, 3 and 4 black, tip of 4th silvery pollinose; proboscis long, 2.2 times as long as subcranial cavity, black. Scutum black, with pair of submedian gray white pollinose stripes converging posteriorly, a pair of lateral gray white pollinose stripes; anterior portion of scutellum gray white pollinose, posteriorly shiny black, setae whitish, sparse, erect; postnotum with lateral gray white areas; wings hyaline, longitudinal veins brown; halter black; foreleg and midleg blackish brown, setae mainly black, hindleg black with basal half of femur yellowish with whitish setae, distally setae black, spines reddish-brown; tibia basally yellowish, distally blackish-brown, setae black, tarsi black. Abdominal tergites shiny black, posterior margins on tergites 1–6 yellow, brown on tergite 8, bulla black, setae long and erect, whitish on tergites 1–2, short and black on 3–7; sternites shiny black, setae long, whitish and erect.

Terminalia.—Reddish-brown, dorsal digitate of gonocoxite tapered, apically acute, directed inward; aedeagus broad basally, wedge shaped, with small flange apically (Fig. 5).

Female.—Length 15.0–15.5 mm. Coloration and structure similar to male except abdominal tergites 4–7 and terminalia orange-brown, tergites 1–4 with yellow posterior transverse margins.

Material examined.—Holotype male, MEXICO: Acapulco, Guerrero, 17 IX 1941, Joseph D. Reed; paratypes, 2 females, same data as holotype. The holotype and paratypes will be returned to the University of Colorado Museum, Boulder.

Etyomology.—We take great pleasure in naming this species for Wendy Meyer, Colorado State University, whose knowledge of entomology is inspiring.

Remarks.—The male of *N. wendyae* can be distinguished from the similar appearing *N. lamia* and *N. sponsor* by the form of the aedeagus (Fig. 5). The female is also similar to *N. sponsor* and can be separated by the blackish brown distal flagellomeres and white setae of the face.

Nemomydas fronki New Species
Fig. 6

Male.—Length 12.0–13.5 mm. Head shiny black, setae erect, black; antennae 3.3–3.5 mm long, black; proboscis short, 0.9 times as long as subcranial cavity, black. Thorax shiny black, setae black, long and erect; wing light brown, veins blackish brown; halter black; legs black, setae long, black. Abdominal tergites black, bulla black, setae black, long, erect on tergites 1–3, long, black, recumbent on tergites 4–7; sternites black, setae black.

Terminalia.—Black, dorsal digitate process of gonocoxite small, originating on in-

ner surface of ventral digitate process; aedeagus slender in lateral view (Fig. 6).

Female.—Length 13–14 mm. Head shiny black, setae short, erect, black; antennae 3.5–3.8 mm, black tinted with brown; proboscis short, 0.8 times as long as subcranial cavity, black. Scutum reddish brown, 3 faint black dorsal stripes, setae black, recumbent; wing light brown, darker brown tinting around blackish brown longitudinal veins; halter black; leg dark brownish black, setae black. Abdominal tergites 1–5 or 6 brownish orange, tergite 6 or 7 black, posterior margins of tergites 4–5 or 6 black, lateral margins of tergites 1–5 black, bulla black, setae very sparse, black, erect; sternites 1–7 blackish brown; terminalia black.

Material examined.—Holotype male, TEXAS: Kenedy Co., 5 mi. S. 10–15 mi. E of Sarita, 25 V 1979, H. E. Evans, A. Hook, W. Rubink. Paratypes: 2 males, 2 females, same data as holotype.

The holotype and one paratype female will be deposited in the CAS and the remaining specimens in the Colorado State University Insect Collection.

Eytomology.—We take great pleasure in naming this species for Dr. W. Don Fronk, Emeritus Professor of Entomology, Colorado State University. He has nurtured numerous students of entomology throughout his distinguished career.

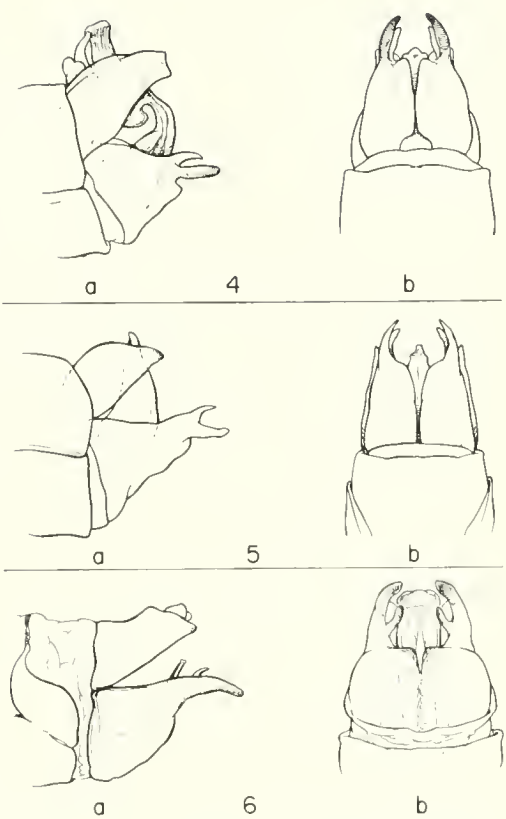
Remarks.—The male of *N. fronki* is easily distinguished from all other species by its totally black coloration (including all setae) and distinctive small dorsal digitate process of the gonocoxite (Fig. 6). The brownish orange abdominal tergites with black pleural margins easily separates the female from all other described females.

Nemomydas tenuipes (Loew)
Fig. 7

Midas tenuipes Loew, 1872: 61. Type locality: California. Holotype male (MCZ #10654), examined.

Leptomydas tenuipes, Johnson, 1926: 142.

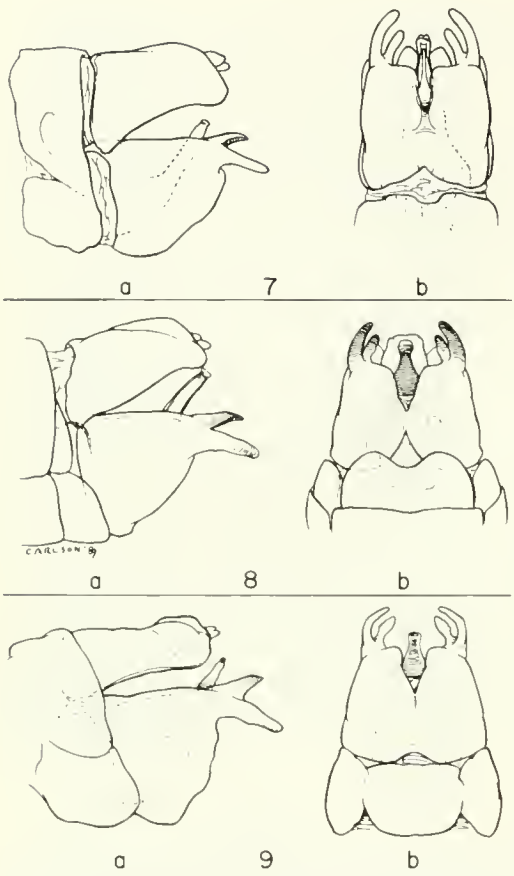
Nemomydas tenuipes, Hardy, 1950: 33.



Figs. 4–6. 4. *Nemomydas sponsor.* Male terminalia, a. lateral, b. ventral. 5. *Nemomydas wendyae,* n. sp. Male terminalia, a. lateral, b. ventral. 6. *Nemomydas fronki,* n. sp. Male terminalia, a. lateral, b. ventral.

Remarks.—Only the male is known and Hardy (1950) presented an excellent description. The abdomen ranges from black to reddish-black. *Nemomydas tenuipes* is readily distinguished from the only other black species, *N. fronki,* by dorsal digitate process of the gonocoxite originating at the base of the ventral digitate process of the gonocoxite (Fig. 7), yellow or white setae on the thorax and tergite 1, and its limited distribution (California and Mexico (Baja California)).

Material examined.—Holotype male, CALIFORNIA: Kern Co., Edwards (MCZ #10654); San Francisco, Presidio Park, 13 VI 1981, W. J. Pulawski, 1 male (CAS); San



Figs. 7–9. 7. *Nemomydas tenuipes*. Male terminalia, a. lateral, b. ventral. 8. *Nemomydas bifidus*. Male terminalia, a. lateral, b. ventral. 9. *Nemomydas intonsus*. Male terminalia, a. lateral, b. ventral.

Diego Co., Hot Springs Mountain Peak, 30 VI 1979, JWB, 1 male (SDNHM). MEXICO: Baja California (Norte), Vic. Fausino, San Juarez, 7 VI 1981, D. K. Faulkner and Brown, 1 male (SDNHM).

Nemomydas bifidus Hardy
Fig. 8

Nemomydas bifidus Hardy, 1950: 22. Type locality: California. Holotype male (CAS), examined.

This species is only known from the holotype male. It closely resembles *N. intonsus* and immaculate male variants (yellow brown tergites lacking the posterior transverse blackish brown bands) of *N. pantherinus*. It may be distinguished from *N. intonsus* by the black setae of the legs and abdomen, and from *N. pantherinus* by the longer proboscis (at least 1.3 times the length of the subcranial cavity) and the stouter aedeagus (Fig. 8). The lateral view of the terminalia illustrated by Hardy (1950, Fig. 5e) is not accurate.

Material examined.—Holotype male: CALIFORNIA: Riverside Co., Idyllwild, VI 1936, E. S. Ross (CAS).

Nemomydas intonsus Hardy
Fig. 9

Nemomydas intonsus Hardy, 1950: 27. Type locality: Pine Valley, California, Holotype male (UK), examined.

Remarks.—Hardy (1950) provides an excellent description of this rare species, known only from the types, and need not be repeated here. The proboscis is moderately developed, 1.3 times length of subcranial cavity.

Material examined.—Holotype male: CALIFORNIA: San Diego Co., Pine Valley, 27 VI 1938, L. W. Hepner (UK); allotype female, same data as holotype (UK).

Nemomydas fumosus Hardy, New Status
Fig. 10

Nemomydas intonsus fumosus Hardy, 1950: 29. Type locality: San Diego Co., California, Holotype male (UK), examined.

Hardy (1950) considered this species to be a variety of *N. intonsus*. It is considered here as a valid species, and can be separated from similar appearing relatives, *N. bifidus* and *N. intonsus* by the blackish brown femora, tergites brownish black with lateral triangular whitish spots on tergites 3–5. The proboscis is 1.6 times length of the subcranial cavity. The terminalia of *N. fumosus* and *N. intonsus* are very similar.

Material examined.—Holotype male, CALIFORNIA: San Diego Co., 7 VI 1929,

P. W. Oman; allotype female, same data as holotype.

Nemomydas pantherinus (Gerstaecker)
Fig. 11

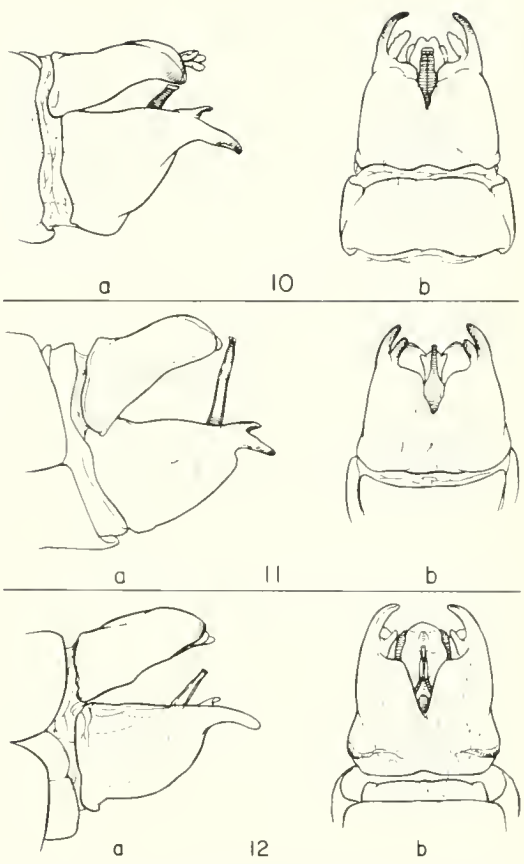
Leptomydas pantherinus Gerstaecker 1868: 85. Type locality: California. Holotype female (Humboldt-Universitat), not examined.

Leptomydas pantherinus, Johnson, 1926: 142.

Nemomydas pantherinus, Hardy, 1950: 30.

Remarks.—This relatively common and quite variable species can be distinguished from other far western, primarily yellow or yellow brown species (*N. intonsus* and *N. bifidus*) by the short proboscis, 0.8–0.9 times as long as subcranial cavity.

Material examined.—CANADA: British Columbia, Oliver, 22 July 1923, P. N. Vroon, 2 males, 4 females (CNC). MEXICO: Baja California Sur, 3 mi NE San Isidro (La Purisima), 2 IV 1985, Bloomfield and D. K. Faulkner, 1 female (SDNHM); Santo Domingo River, 3–4 VIII 1979, Brown and D. K. Faulkner, 1 male (SDNHM); same except Santo Domingo (ruins), 1 male (SDNHM). UNITED STATES, CALIFORNIA: Humboldt Co., Strong Std., 14 VIII 1938, B. P. Bliven, 1 female (CAS); Van Duzen River, 19 VII 1936, B. P. Bliven, 5 males, 5 females (CAS); Inyo Co., Hoton Creek Campground, Hwy 395, 4 VII 1981, R. M. Brown, 1 female (CAS); Los Angeles Co., N. Long Beach, 5 VIII 1938, A. Mallis, 1 female (CAS); Orange Co., Irvine, 23 VIII 1960, D. Magoi, 1 male (CAS); Santa Ana, 10 VIII 1964, J. Wilcox, 1 female (CAS); Riverside Co., Herkey Creek, San Jacinto Mtns., 20 VI 1940, 1 male (CAS); Temecula, 30 VI 1956, J. Wilcox, 1 male, 1 female (CAS); Temecula, 4 VII 1950, J. W. MacSwain, 2 males (CNC); San Bernardino Co., Barstow, 24 VI 1914, J. R. Haskin, 1 female (CAS); El Cajon, 2 VII 1974, 1 female, 1 male (CAS); San Bernardino, 2 IX 1895, W. G. Wright, 1 female (CAS); Victorville, 2.5 mi. NW at Mojave,



Figs. 10–12. 10. *Nemomydas fumosus*. Male terminalia, a. lateral, b. ventral. 11. *Nemomydas pantherinus*. Male terminalia, a. lateral, b. ventral. 12. *Nemomydas solitarius*. Male terminalia, a. lateral, b. ventral.

9 VIII 1983, D. Williams, 1 female (CAS); nr. Wrightwood, 21 VII 1954, F. M. Hull, 1 female (CNC); San Diego Co., Bordenfieldis Bay, 6 VIII 1982, B. Parks, 1 female (SDNHM); Lakeside, 20 VII 1965, J. Heppner, 1 male (FSCA); Mission Gorge (dam), 15 VII 1978, L. Guidry, 4 males (SDNHM); San Diego, 16 IX 1890, F. E. Blaisdell, 2 males, 1 female (CAS); San Diego, 2–5 VIII 1954, H. E. and M. A. Evans, 1 male, 1 female (CAS); San Diego, 12–13 VII, W. S. Wright, 2 males, 1 female (CAS); Tulare Co., Porterville, 6 VIII 1959, E. Ball, 1 male (FSCA); same but 25 VII 1957, 1 female (FSCA); Springville, 25 VII 1957, E.

Ball 1 female (FSCA); Ventura Co., Foster Park, 1 VII 1959, J. L. Bath, 2 males, 1 female (CAS).

Nemomydas solitarius (Johnson)
Fig. 12

Leptomydas solitarius Johnson, 1926: 142. Type locality, Colorado, Holotype male (MCZ #7391), examined.
Nemomydas solitarius, Hardy, 1950: 32.

Hardy (1950) suggested that this species ". . . may possibly be the same . . ." as *N. pantherinus*. *Nemomydas solitarius* is known only from the holotype male, apparently collected in "Col" with no further data. Despite extensive collecting in Colorado, no additional specimens have been collected for study. It is more similar to *N. bifidus*, *N. intonsus*, and *N. fumosus* than *N. pantherinus*, and can be distinguished from these species by the dorsal digitate process of the gonocoxite originating on the inner face of the ventral process (Fig. 12).

The proboscis is missing from the holotype. Johnson's (1926) description omitted any reference to the relative length of this structure. Hardy (1950) evidently considered the ". . . mouthparts conspicuously short, scarcely, if at all, extended beyond the oral margin . . ."

Material examined.—COLORADO: Holotype male (MCZ #7391).

Nemomydas venosus (Loew)
Fig. 13

Midas venosa Loew, 1866: 15. Type locality: Texas. Holotype male (MCZ #10653), examined.
Leptomydas venosus, Johnson, 1926: 142.
Nemomydas venosus, Hardy, 1950: 34.

Remarks.—The large thumb-like ventral process of the gonocoxite (Fig. 13) easily distinguishes the male of this widespread species. There are both light and dark phases of both sexes, especially with females. Pairs taken in copula have been mixed. Many of the past misidentifications, especially for *N. brachyrhynchus* and *N. pantherinus* (see Curran (1965)), have been due to this color variability. The light form of the female may be confused for these two species and characters of separation are given under *N. brachyrhynchus*. The dark form cannot be confused with any other species.

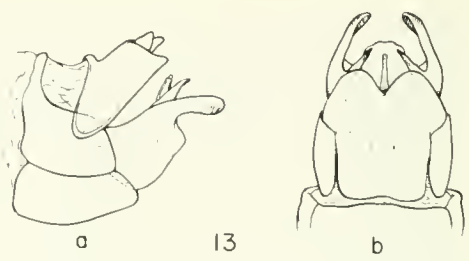
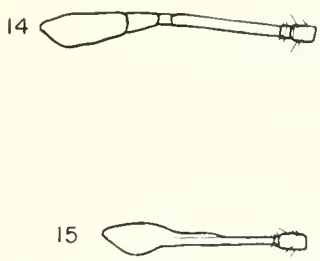


Fig. 13. *Nemomydas venosus*. Male terminalia, a. lateral, b. ventral.

Material examined.—MEXICO: Chihuahua, 6 mi. S. Villa Matamoros, 21 VII 1967, R. C. Gardner, C. R. Kovacic, K. Lorenzen, 2 males, 2 females (CAS); Sinaloa, Baviri (playa) W Los Mochis, 9 IX 1986, D. K. Faulkner, Bloomfield, 1 male (SDNHM); Sonora, La Aduana, W. of Alamosa, 18 VIII 1964, T. E. Irwin, 1 male (CAS). UNITED STATES, ARIZONA: Cochise Co., Chiricahua Natl. Mon., 11 VIII 1962, J. Wilcox, 1 male (CAS); 3 mi. NE Coronado Natl. Mon., 17 VIII 1966, R. L. Westcott, 1 female, 1 male (CAS); 8 mi. E Douglas, 4 VIII 1958, R. M. Bohart, 1 female (CAS); same except 8 VIII 1964, P. M. Marsh, 1 male; Montezuma Canyon, Huachuca Mtns., 19 VIII 1968, G. R. Ballmer, 1 female (CAS); Wilcox Dry Lake, 25 VIII 1967, F. G. Andrews, 1 male 3 females (CAS); same except E. I. Schlinger, 1 female 1 male (CAS); same except D. J. Culver, 1 male (CAS); Coconino Co., Oak Creek Canyon, 15 VI 1936, G. P. Engelhardt, 1 male (CAS); Gila Co., Globe, D. K. Duncan, 1 female (CSU); Pima Co., Florida Wash, 21 VIII 1979, D. K. Faulkner, 3 males (SDNHM). COLORADO: Phillips Co., Holyoke, 26 VII 1946, M. T. James, 1 male (CSU); Weld Co., Roggen, 21 VIII 1976, H. E. Evans, 1 male



Figs. 14, 15. *Nemomydas bequaerti*. Antenna. 15. *Nemomydas brachyrhynchus*. Antenna.

(CSU); same except 24 VIII 1976, 2 males; same except 4 VIII. 1977, 1 male; same except 17 VIII 1982, 5 males, 4 females; Roggen, 8 IX 1933, M. T. James, 1 male (CSU); same except 31 VIII 1938, 9 males, 5 females; same except 15–18 VIII 1941, 1 male, 1 female; KANSAS, Kearny Co., Lakin, 28 VIII 1951, R. R. Dreishbach, 1 male (UCB); NEW MEXICO, Chaves Co., 14 VIII 1955, R. R. Dreisbach, 1 male (MSU); Grant Co., 29 VIII 1935, R. T. Kellogg, 3 males (CAS); Silver City, 14 IX 1935, B. T. Kellogg, 1 male, 1 female (CAS). TEXAS: Holotype male, Texas (MCZ #10653, terminalia missing); Jeff Davis Co., 24 mi. NW Ft. Davis, 24 XI 1965, R. W. Thorp, 1 female (CAS); Kleberg Co., 20 mi. SE Kingsville, 1 V 1985, W. J. Pulawski, 1 male (CAS); Riviera Beach, 28 V 1979, H. Evans, A. Hook, W. Rubink, 1 M (CSU).

Nemomydas panamensis (Curran), *nomen dubium*

Nomoneura panamensis Curran, 1934: 165. Type locality: Panama, Canal Zone, Bruja Point.

Nemomydas panamensis, Papavero and Wilcox, 1968: 34.11.

Curran (1934) never published a formal description for this name, and illustrated only the head. Papavero and Wilcox (1968) considered the name available (authors cited Article 16 (vii) (1964 Code). However, this name was published in 1934, therefore does not satisfy Article 13 (1985 Code). An attempt was made to locate the two males referred to by Papavero and Wilcox (1968). Curran was at the CNC from 1923 to 1928 and from 1928, to 1960 at the AMNH. Curators of these museums (D. Grimaldi, AMNH) and B. E. Cooper, CNC) could not locate these two specimens in their respective collections. We therefore consider this name as a *nomen dubium*.

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NEW NORTH AMERICAN *COLOBAEA*, WITH A PRELIMINARY ANALYSIS OF RELATED GENERA (DIPTERA: SCIOMYZIDAE)

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Abstract.—Two new species of *Colobaea* (Diptera: Sciomyzidae) are described: **C. canadensis** from Manitoba, Canada, and **C. montana** from Montana, United States. The male genitalia, wings, and antennae are illustrated; the distributions, along with that of *C. americana* Steyskal, are shown in a map; and a key to the world species is included. The major characters of the genera *Colobaea, Pherbellia, Pteromicra,* and *Ditaeniella* are compared and characterized as plesiomorphic or apomorphic, as an aid in determining the generic placement of the new species. *Pherbellia trivittata* (Cresson), *P. parallela* (Walker), and *P. patagonensis* (Macquart) are reassigned to *Ditaeniella.*

Key Words: Flies, *Ditaeniella, Pteromicra, Pherbellia,* taxonomy, systematics, identification

Although the classification of the Sciomyzidae has become well established over the past three decades, new species are continually being discovered, particularly the smaller, rarer, and less conspicuous species.

The genus *Colobaea* Zetterstedt consists primarily of small, black and yellow flies and includes the smallest (less than 2 mm) species of Sciomyzidae, *Colobaea americana* Steyskal (1954). Prior to this study one species was described from the Nearctic Region and seven were described from the Palaearctic Region. There is one undescribed species from Pakistan, Afghanistan, and Iran and one from Nigeria.

Species of *Colobaea* were among the first for which there was at least circumstantial evidence (provided over 60 years ago) that the larvae of Sciomyzidae feed on mollusks. Lundbeck (1923) reared adults of *C. pectoralis* (Zetterstedt) and *C. punctata* (Lundbeck) from puparia found in floating shells of small aquatic snails in Denmark. Rozkošný (1967) provided brief descriptions of the puparia of *Colobaea distincta* (Meigen) and *C. pectoralis,* and Knutson et al. (1973) reared an undescribed species of *Colobaea* in Iran and presented the essential aspects of the life cycle (as *C. iranica* Knutson, *nomen nudum*). Knutson and Bratt (in preparation) have reared the Palaearctic species *C. bifasciella* (Fallén), *C. pectoralis,* and *C. punctata,* the Nearctic species *C. americana,* and the undescribed species from Iran through their complete life cycles and will describe all of their immature stages.

Despite their apparent restriction to freshwater habitats where there are various small species of non-operculate snails, the

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Table 1. Character states of major generic features of *Colobaea* and related genera.

	Colobaea	*Pteromicra*	*Ditaeniella*	*Pherbellia*
1	+ (−)	−	−	−
2	+ (−)	−	−	−
3	+	− (+)	−	−
4	+ (−)	−	−	− (+)
5	+ (−)	−	−	−
6	−	+ (−)	−	−
7	−	+ (−)	−	−
8	−	+	−	−
9	−	+ (−)	+	−
10	−	−	+ (−)	−
11	−	−	+	− (+)
12	−	−	+	−
13	−	−	+	−

List of characters (+ = apomorphic state, − = plesiomorphic state; exceptions noted in parentheses):

1. Arista with some dorsobasal hairs slightly to much longer than ventrobasal hairs (same length in *C. canadensis*).
2. Vein Sc ending close to anterior branch of R_1 (except in *C. canadensis*).
3. Vein A_1 + CuA_2 evanescent apically (variable in *Pteromicra leucothrix* Melander).
4. Anterior surstylus with characteristic peglike processes [absent in *C. canadensis*; present in *Pherbellia mikiana* (Hendel)].
5. Hypandrium with narrow, long posterior process (except in *C. bifasciella*).
6. Frons entirely shining (tomentose in an undescribed species of *Pteromicra* from Japan and India).
7. Fore femur with pecten (absent in *Pteromicra anopla* Steyskal).
8. Hypandrium with pair of pubescent lobes in posteroventral position.
9. Only one fronto-orbital seta [two pairs in *Pteromicra angustipennis* (Staeger) and *P. leucopeza* (Meigen)].
10. Prosternum haired (hairs absent in *D. trivittata*).
11. Inner posterior margin of hind coxa with several hairs (present in *Pherbellia seticoxa* Steyskal).
12. Anterior surstylus considerably reduced.
13. Paramere with conspicuous apical spines.

species of *Colobaea* are broadly distributed. *Colobaea* is most abundant and species rich in Europe and species are also known from Central Asia, Pakistan, Iran, and northern Nigeria. In North America, *Colobaea* ranges from Montana to Manitoba, Quebec, and New York. In his recent review, Rozkošný (1984a) characterized the genus, described a new species from Sweden and Finland, and presented a key to the species. Rozkošný (1984b) illustrated the terminalia of all the species known from Fennoscandia and Denmark. The male genitalia of *C. punctata* were illustrated by Rivosecchi and Prigioni (1980).

To date, the only described Nearctic representative of *Colobaea* is *C. americana* Steyskal. The two North American species described below also apparently belong to *Colobaea*; *C. montana* Knutson and Orth has all of the recognized apomorphic characteristics of the genus, but the placement of *C. canadensis* Knutson and Orth is less certain. Table 1 shows the character states of the major generic features (primarily as recognized by Rozkošný 1984b) of *Colobaea* and the three related genera, *Pherbellia* Robineau-Desvoidy, *Pteromicra* Lioy, and the recently resurrected *Ditaeniella* Sack (Rozkošný 1987); however, we have not been able to identify any synapomorphies for these four genera.

Key to Species of *Colobaea* Zetterstedt (modified from Rozkošný 1984a)

1. Ground color of mesonotum brownish yellow; wing with two transverse dark bands (Palaearctic) ..... *C. bifasciella* (Fallén)
− Mesonotum black; wing without bands 2
2. Proepisternum and anepisternum both, at least in part, yellow 3
− Proepisternum and anepisternum usually entirely black like rest of thorax 7
3. Thorax mainly black, but with some yellow on proepisternum and anepisternum 4
− Thorax more extensively yellow 5
4. Dorsobasal hairs of arista distinctly longer than ventrobasal hairs (Nearctic) ..... *C. americana* Steyskal
− Dorsobasal hairs of arista not longer than ventrobasal hairs (Nearctic) ..... *C. canadensis* Knutson and Orth, n. sp.
5. Third antennal segment 3 times as long as width at base; both crossveins of wing conspicuously infumated (Palaearctic) ..... *C. limbata* (Hendel)
− Third antennal segment 2 times as long as width at base; crossveins not infumated 6
6. Upper margin of anepisternum with complete dark stripe (Palaearctic) ..... *C. pectoralis* (Zetterstedt)
− Upper margin of anepisternum only with rounded black spot below anterior notopleural seta (Palaearctic) ..... *C. punctata* (Lundbeck)

7. Third antennal segment 3 times as long as wide basally; both crossveins of wing distinctly infumated (Palaearctic) ..... *C. beckeri* (Hendel)
– Third antennal segment 2 times as long as wide basally; crossveins not infumated 8
8. Third antennal segment and arista black; anterior margin of frons extensively yellow 9
– Third antennal segment white at base, arista white; frons entirely black (Palaearctic) ..... *C. distincta* (Meigen)
9. Propleuron always black; only last tarsal segment of foreleg white (Palaearctic) ..... *C. nigroaristata* Rozkošný
– Propleuron usually black, occasionally yellowish; last two tarsal segments of foreleg white (Nearctic) . *C. montana* Knutson and Orth n. sp.

Colobaea canadensis Knutson and Orth, New Species
Figs. 1–4, 13

Male.—Body length, 3.0 mm. Head slightly wider than high, width of gena about ¼ height of eye. Face and gena with short, whitish tomentum. Frons narrowed anteriorly, yellowish tomentose, with many short, black bristles evenly distributed over anterior ¼. Ocellar triangle shiny black, not extending as far as anterior end of shiny, brownish fronto-orbital plates. No orbito-antennal spot, very narrow stripe of fine, whitish tomentum extending along upper orbital margin and fading out near posterior fronto-orbital bristle. Pair of shallow depressions, with dense whitish tomentum, on either side of midline near top of occiput. Occiput blackish brown around foramen. Postgena yellowish to tan. Two pairs of rather strongly recurved fronto-orbital bristles, anterior pair slightly shorter than posterior pair; ocellar, postocellar, and inner and outer vertical bristles well developed and subequal in length. Many short, black setae on lower ½ of gena, finer anteriorly and extending onto lower parafacial. Short black setae also on ocellar triangle, along outer margin of fronto-orbital plates, and above occipital foramen. Lateral margins of occiput and postgena with several rows of irregularly dispersed, short, stout setae, no such setae mid-dorsally on occiput. Antennae light yellow to yellowish brown; segment 3 oval, darkened dorso-apically. Arista brown, lighter basally, plumosity moderately dense, semi-recumbent, about as long as width of arista at base, dorsobasal hairs not setose or longer than ventrobasal hairs. Palpus yellowish white with many strong bristles, especially apically; labella yellowish.

Thorax black with faint gray tomentum, postpronotal lobe slightly brownish. Pleura mostly brownish black, lower parts with strong whitish tomentum; ventral part of propleuron and anteroventral part of anepisternum yellowish. Thoracic chaetotaxy: 1 pro-episternal, 1 postpronotal, 1 presutural intra-alar bristle, 2 notopleural, 1 supra-alar, 2 subequal postalar, 2 dorsocentral (anterior pair slightly shorter, somewhat mesad of posterior pair and caudad of supra-alar), 1 weak prescutellar acrostichal behind dorsocentral, 1 basal scutellar, and 1 subequal apical scutellar. A few fine hairs posterior to pro-episternal seta. Anepisternum bare. Anepimeron with two fine bristles anteroventrally, no vallar (subalar) bristles. Posterior half of katepisternum with dense coat of long, fine hairs over most of surface, several bristles along upper margin, two exceptionally long hairs posterodorsally, well developed bristles ventrally. Pro-episternum bare.

Front coxa slightly less than ¾ length of fore femur, yellow with whitish tomentum, several strong bristles below middle on external margin and one or two near apex; midcoxa brownish dorsolaterally, yellowish ventrally; hind coxa yellowish, bare on posterodorsal surface. Fore femur robust, shiny black, with two irregular rows of 6–10 bristles on dorsal surface, bristles of anterior row larger than those of posterior row; mid-femur with anterior bristle beyond middle and three short hairlike bristles in row at posteroventral apex. Hind femur with two strong bristles posterodorsally, ventrally with dense coat of short bristles; fore tibia black except extreme base yellowish, with dense coat of greyish tomentum; mid and hind tibiae yellowish. Tarsi entirely yellow

except basal segment of fore tarsus darker on sides.

Wing length, 2.8 mm. Membrane yellowish, hyaline; longitudinal veins yellow, crossveins darker and slightly infuscated. Pterostigma large, R_1 terminating beyond r-m crossvein, r-m crossvein at midlength of discal medial (dm) cell, vein $A_1 + CuA_2$ not reaching margin of wing. A few short setae on R_{4+5} beyond r–m crossvein and on CuA_1 before dm-cu crossvein. Halter, calypter, and calyptral ciliae yellowish white.

Abdominal terga shiny dark brown with faint silvery tomentum, posterior margins yellowish. Bristles longest on posterolateral margins of fifth tergum. Syntergosternite 6–8 well developed, anterior margin of sixth sternum darkly pigmented, extending across venter to dextral side of abdomen. Terminalia shiny blackish brown. Andrium as in Figs. 1 and 2. Ventral margin of epandrium not oblique posteriorly. Anterior surstylus flat, with one rounded, posterolaterally directed lobe and one rounded, ventrally directed lobe; without darkly pigmented, mesal peglike processes. Posterior surstylus broad, scooplike, apex curved at almost right angle to meson; apices of posterior surstyli overlapping. Anterior end of hypandrium straight, broad. Ejaculatory apodeme equal in length to aedeagal apodeme, sinuate, plate rather small. Posterior arms of aedeagal apodeme broad, moderately elongate.

Female.—Body length, 3.0–3.2 mm. Frons only slightly narrowed anteriorly. Subshiny orbital plates light brown, only slightly darker than yellowish frons. Occiput brownish, cervical area yellowish. No strong hairs at base of arista.

Postpronotal lobe yellow. Pro-episternum extensively yellow below spiracle, anepisternum faintly yellow along upper part of posterior margin; anepimeron mottled yellow and brown. Prescutellar acrostichal bristles not larger than other acrostichals. Outer postalar a little larger than inner postalar. Anepimeron with three or four fine bristles. Katepisternal hairs and bristles shorter, sparser than in male.

Abdominal terga lighter than in male, posterior margins narrowly to broadly yellow. Cercus yellow.

Midcoxa brownish to yellowish laterally. One specimen with three posterodorsal and two anterodorsal bristles apically on hind femur. Fore tarsus black to dark brown, apical segment lighter; mid and hind tarsi yellow.

Wing length, 2.9–3.1 mm.

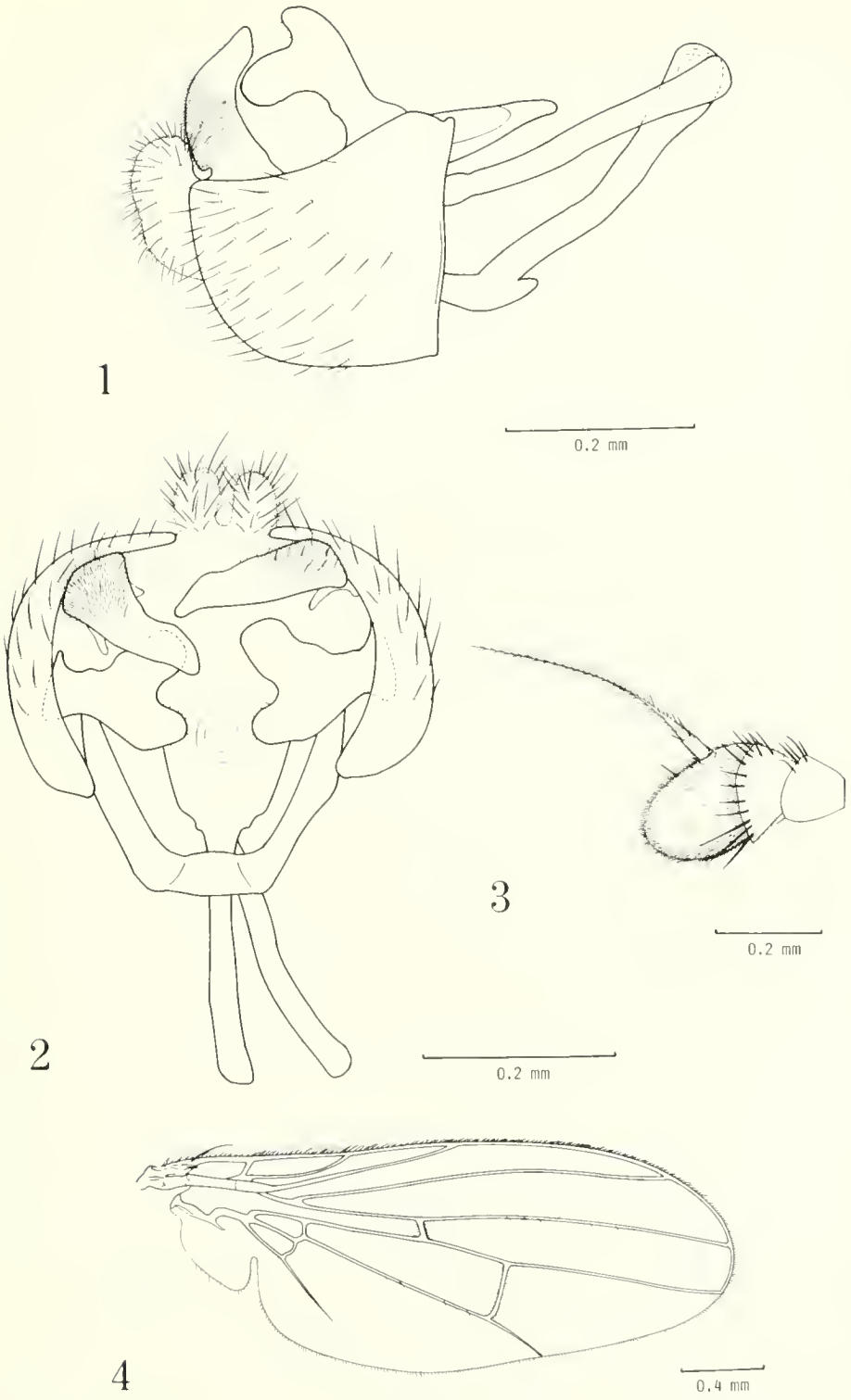
Diagnosis: Colobaea canadensis differs from all other species of *Colobaea* by the dorsobasal hairs on the arista being no longer than the ventrobasal hairs, and the lack of peglike processes on the anterior surstylus. It most resembles *C. bifasciella* in that both species have a dull, tomentose, bristled, yellow frons; a similarly shaped head; two pairs of postalar bristles; and R_1 extending to the level of the r–m crossvein. These two species can be readily distinguished, however; *C. canadensis* has a mainly shiny black body and unpatterned wings, whereas *C. bifasciella* has a yellow body with black markings and patterned wings.

Type specimens.—Holotype male: Canada, Manitoba, Mile 505, Hudson Bay Ry.; 13 June 1952; J. G. Chillcott; ecological data F-D; in Canadian National Collection, Ottawa. Allotype: female, Canada, Manitoba, Mile 504, Hudson Bay Ry.; 21 June 1952; J. G. Chillcott; ecological data F-H, along RR; in Canadian National Collection. Paratype: female, Canada, Manitoba, Warkwork Cr. nr. Churchill; 7 July 1952; J. G. Chillcott, ecological data F-D; LVK Slide Nos. 7044 and 7055, in United States National Museum of Natural History. Distribution map, Fig. 13.

Colobaea montana Knutson and Orth, New Species

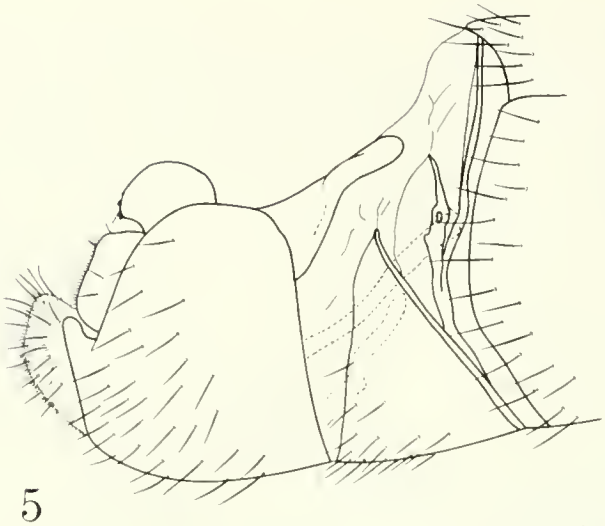
Figs. 5–13

Male (female unknown): Body length, 3.0 mm. Head ¼ narrower than height; height of gena about ⅕ height of eye. Face shiny yellow, narrow, with strong median carina; clypeus rounded and somewhat produced



Figs. 1, 2. *Colobaea canadensis*, holotype male. 1, Postabdomen, sinistral view, inverted. 2, Postabdomen, ventral view.

Figs. 3, 4. *Colobaea canadensis*, paratype female. 3, Left antenna. 4, Right wing.



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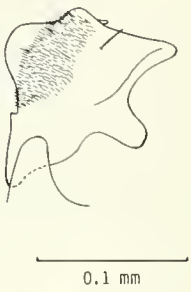

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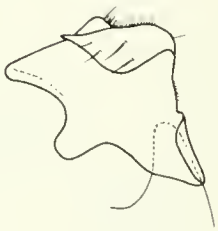

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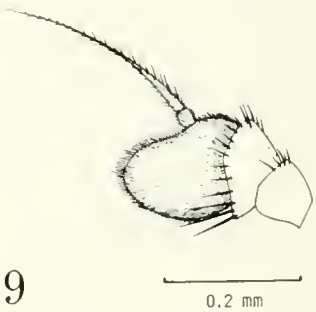

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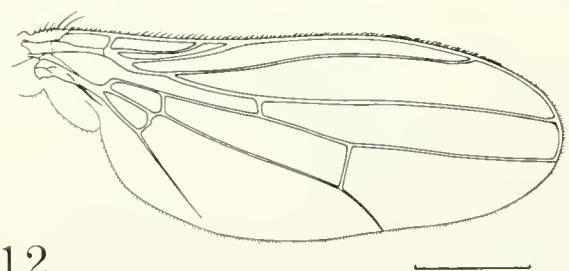

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anteriorly. Gena yellowish white. Frons strongly narrowed just above antenna, densely matt-tomentose, mostly black, yellowish anteriorly, yellow area extended triangularly toward anterior ocellus. Ocellar triangle subshiny black, not prolonged anteriorly; fronto-orbital plates shiny black; tomentose whitish patch between base of antenna and orbital plate. Occiput shiny black over most of surface; postgena whitish yellow. Two subequal, erect fronto-orbital bristles; ocellars and inner and outer verticals well developed, longer than fronto-orbitals; postocellars smaller than fronto-orbitals. Short, black setae in two irregular rows along lower margin of gena extending along groove between gena and face to anteroventral angle of eye; on anterolateral edge of yellowish part of frons; sparsely between ocellar and postocellar bristles; and in patch above foramen. Upper occipital margin with weak setae only. First and second antennal segments yellow; second segment with weak bristles on dorsal edge, around apical margin, and several strong bristles ventro-apically; third segment ovoid, black, slightly brownish at base of arista on external surface, more extensively yellowish brown basally on inner surface. Arista brown with a few short, rather thick hairs; some dorsobasal hairs slightly spinose and longer than ventrobasal hairs; all hairs shorter than width of arista at base. Palpus yellowish white, with a few weak bristles; labella yellowish white.

Thorax including scutellum entirely black except in the Swan Lake specimen, propleuron yellowish; no silvery tomentum. Prosternum yellow. Thoracic chaetotaxy: 1 short pro-episternal, 1 postpronotal, 1 post-humeral, 2 notopleural, 1 supra-alar, 1 post-alar, 2 dorsocentral (anterior pair slightly shorter), 1 weak prescutellar acrostichal, 1 basal scutellar, 1 apical scutellar. Anepisternum bare, anepimeron with three or four fine bristles anteriorly, no vallar bristles. Katepisternum with one strong bristle mid-dorsally and a few hairs posteroventrally, well developed bristles midventrally. Prosternum bare.

Fore coxa ⅔ length of fore femur, subshiny yellowish white, one or two strong bristles below middle on external margin and several apically; mid and hind coxae yellowish, darker dorsally; hind coxa bare above. Fore femur robust, basal ½ to ⅔ yellowish, remainder black, more extensively darkened along dorsal surface, two irregular rows of 5–8 bristles on dorsal surface; mid-femur yellow, one anterior bristle beyond middle, three hairlike bristles in row at posteroventral apex; hind femur mostly yellowish, brownish apically, one strong bristle anterodorsally; ventrally with double row of widely spaced bristles. Fore tibia black, mid and hind tibiae yellow. Fore tarsus with basal segment black, segments 2 and 3 brownish, segments 4 and 5 yellowish; mid and hind tarsi yellowish, apical segment darker.

Wing length, 1.9–2.1 mm. Membrane grayish hyaline, longitudinal veins yellowish to brownish, crossveins not infuscated. Pterostigma small, Sc ending close to R_1; R_1 terminating basad of crossvein r-m; r-m slightly beyond midlength of cell dm; $A_1 + CuA_2$ extending almost to margin of wing. Halter, calypter, and calyptral ciliae yellowish white.

Abdominal terga and sterna shiny black, posterior margins of posterior sterna nar-

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Figs. 5, 6. *Colobaea montana*, holotype male. 5, Postabdomen, sinistral view, inverted. 6, Postabdomen, ventral view.

Figs. 7–12. *Colobaea montana*, paratype male, 4 miles east of Bigfork, Montana. 7, 8, Posterior surstylus, sinistral view, inverted. 7, Outer surface. 8, Inner surface. 9, Left antenna. 10, 11, Anterior surstylus, sinistral view, inverted. 10, Outer surface. 11, Inner surface. 12, Right wing.

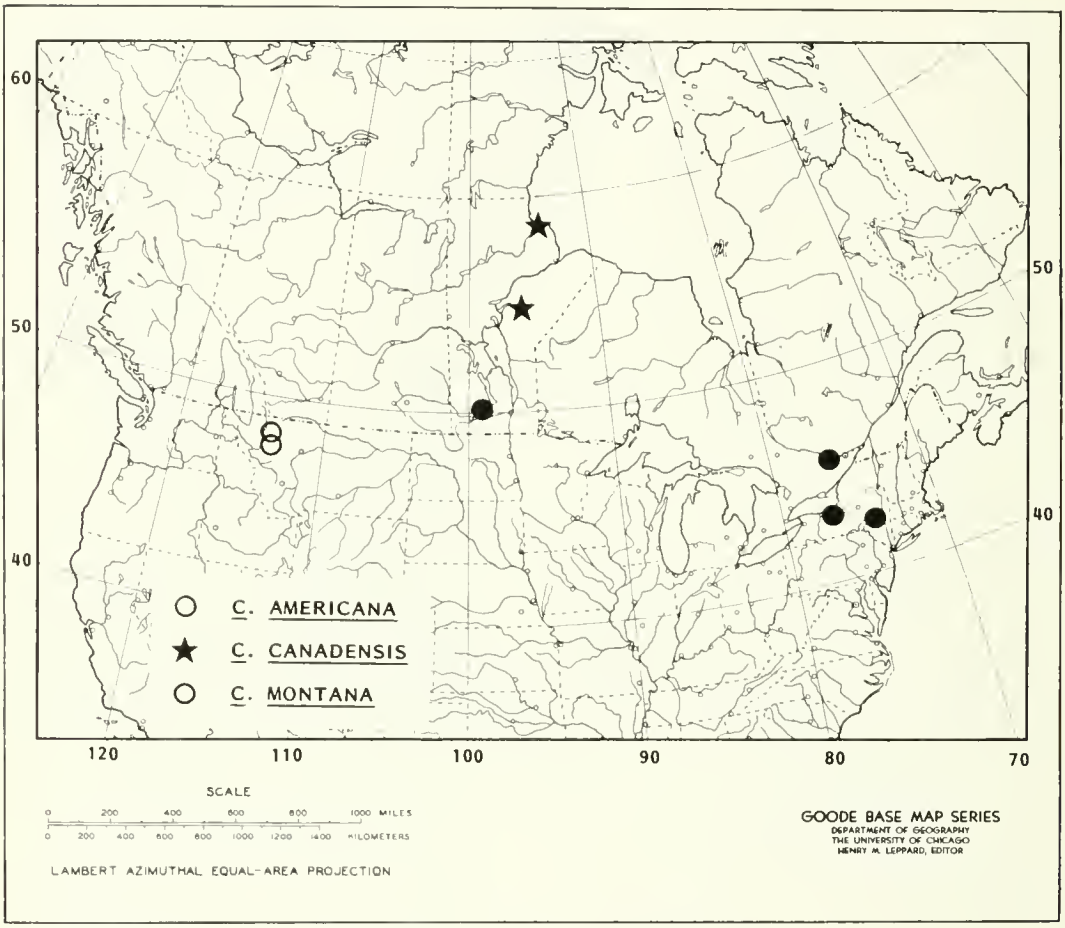

Fig. 13. Collection sites for *Colobaea americana, C. canadensis,* and *C. montana.*

rowly yellow; only posterior terga with a few strong, black bristles. Syntergosternite 6–8 well developed; anterior margin of sixth sternum darkly pigmented, extending across venter to dextral side of abdomen. Andrium as in Figs. 5 and 6. Epandrium with ventral margin oblique posteriorly, with lobelike process midlaterally on posterior margin. Anterior and posterior surstyli widely separated. Anterior surstylus clublike, curved mesally and approximate, posteromesal margin and posterodorsal surface with dense coat of short, thick, peglike processes. Posterior surstylus as in Figs. 7 and 8. Anterior end of hypandrium broad, rounded. Aedeagal apodeme lightly pigmented, broadened posteriorly, twice as long as ejaculatory apodeme.

Diagnosis: With a mostly matt black frons and R_1 terminating considerably basad of r–m, *C. montana* is more similar to *C. americana, C. nigroaristata* Rozkošný, *C. punctata,* and related species than it is to *C. bifasciella* and *C. canadensis.* Although in the key to species, which is based on external characters, *C. montana* and *C. nigroaristata* run out in the same couplet, males can be readily separated by the internal structures of their terminalia—most notably the shape of the posterior surstylus (see

Rozkošný 1984a). The shape of the posterior surstylus, short dorsobasal hairs on the arista, and lack of silvery tomentum along the margin of the eye distinguish *C. montana* from *C. americana,* the only other species of *Colobaea* likely to occur with *C. montana.*

Type specimens.—Holotype male and 2 male paratypes: United States, Montana, 4 miles east of Bigfork; 29 July 1965; B. A. Foote; one male paratype: Montana, 20 mi. south of Swan Lake, 20 August 1968; B. A. Foote. All specimens in the United States National Museum of Natural History. Distribution map, Fig. 13.

Comparison of *Colobaea* with Other Genera

A comparison of the character states of major generic features of *Colobaea* and the related genera *Pteromicra, Ditaeniella,* and *Pherbellia* is shown in Table 1. *Pherbellia* is probably polyphyletic. In the process of making these comparisons, it became clear that one group of "*Pherbellia*" species should be transferred to the genus *Ditaeniella. Ditaeniella* was proposed by Sack (1939) for the Palaearctic species *Sciomyza grisescens* Meigen. Most subsequent authors placed *S. grisescens* in *Sciomyza* or *Pherbellia.* Steyskal (1963) noted the similarities (especially in the male genitalia) of *S. grisescens, S. humilis* Loew (Nearctic) (= *S. parallela* Walker), and *S. patagonensis* Macquart (Neotropical) and placed these species in the *Pherbellia grisescens* group. He noted, "The andrium is of a rather special type in the Sciomyzinae and may be the basis for eventually segregating the group nomenclaturally from *Pherbellia.*" Rozkošný (1987) resurrected *Ditaeniella* as a valid genus, including *S. grisescens.* We propose the following new combinations:

Ditaeniella parallela (Walker) 1853 (Nearctic and Neotropical).

Ditaeniella patagonensis (Macquart) 1851 (Neotropical).

Ditaeniella trivittata (Cresson) 1920 (Nearctic).

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A NEW SPECIES OF *DIORYCTRIA* (PYRALIDAE: PHYCITINAE) FROM MEXICO

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Abstract.—**Dioryctria cuitecensis** n. sp. from the state of Chihuahua is described. A habitus photograph of the male holotype, and drawings of the male and female genitalia of *D. cuitecensis*, and a key to Mexican species of *Dioryctria* are included.

Key Words: taxonomy, *Dioryctria cuitecensis*, *Dioryctria* key

Larvae of all species of *Dioryctria* Zeller (Pyralidae) are associated with conifers. Because pines and their relatives are a common group of trees in many parts of Mexico, numerous species of *Dioryctria* may be expected in this part of North America. As recently as the middle of this century, however, only one species of these phycitines was recorded from the Republic (Heinrich 1956), probably because of limited collecting. Within the last several decades entomologists from the United States and Canada have more extensively light trapped in Mexico, and thereby greatly increased the number of Mexican Lepidoptera in collections. In addition, the Mexican Division of Forest Sciences, in cooperation with the Forest Service of the United States Department of Agriculture, has made a concerted effort to collect and rear cone insects in Mexico (Hedlin et al. 1981, Cibrián-Tovar et al. 1986). As a result, the number of known species of *Dioryctria* in Mexico increased to ten. Recently, the following additional Mexican species in the genus has come to my attention.

Dioryctria cuitecensis, NEW SPECIES
(Figs. 1, 2–4)

Diagnosis.—*D. cuitecensis* is a large, dark, rather uniformly marked species (Fig. 1). The transverse lines are very obscure, consisting of only a very few white-tipped scales, the discal spot is only slightly paler than the surrounding scales, and the black scales that characteristically accent the transverse lines are for the most part diffuse. The male and female genitalia of *D. cuitecensis* are similar to those of *D. cambiicola* Dyar, a species occurring in the United States, however, the forewing of the latter species has distinct silvery white transverse lines accented with adjacent patches of black, and distinct patches of silvery white scales inside the subbasal scale ridge, on the discal spot, between the discal spot and the postmedial line, and just before the terminal line.

Description.—*Head:* Frons and vertex brown, fuscous or reddish brown. Labial palpus reaching above vertex in both sexes, mostly brown to fuscous with very few white-tipped scales. Maxillary palpus squamous, mostly brown and fuscous. Antenna of male filiform with abundant, short sensilla trichodea. *Collar:* Brown or reddish brown. *Thorax:* Dorsum brown to reddish brown, in part suffused with fuscous or black. Forewing: Length 15.5–17.0 mm; above with distinct, strongly raised scales forming subbasal and antemedial patches; postmedial patch of raised scales also present but scales noticeably less elevated than those of

Fig. 1. *Dioryctria cuitecensis*, ♂, Holotype. Scale line = 1.0 mm.

basal patches; additional smaller patches of raised scales at base and at discal spot; ground color brown; antemedial line very obscure, usually consisting of a few pale brown or white-tipped pale brown scales in inner half; postmedial line also very weak; diffuse, indistinct patches of fuscous and black scales in median area and along costa; numerous red, orangish red or reddish brown-tipped scales in basal, subbasal, inner median and terminal area (usually a distinct rust color in basal and subbasal area including the raised subbasal patch of scales); discal spot obscure, only slightly more pale than surrounding scales; terminal line fuscous to black; undersurface of male with short, basal, pale gray subcostal streak. *Hindwing:* Above, dark brownish gray. *Male genitalia:* (Figs. 2, 3) similar to male genitalia of *Dioryctria cambiicola* except juxta of *D. cuitecensis* noticeably smaller than that of *D. cambiicola*. *Female genitalia:* (Fig. 4) similar to female genitalia of *D. cambiicola*.

Type material.—Holotype male, Cuiteco, Chih, Mex, VIII 27 1969, T. A. Sears, R. C. Gardner, C. S. Glaser, genitalia slide 2090 HHN, deposited in the Bohart Museum of Entomology, University of California, Davis. Paratypes: three females, same collection data as for holotype except IX 3 1969, IX 8 69, genitalia slide 2091 HHN. Paratypes deposited in collections of University of California, Davis, National Museum of Natural History, Washington, D.C. and North Carolina State University, Raleigh.

Distribution and life history.—Known only from southwestern Chihuahua, Mexico. Host plant(s) and behavior of larvae, unknown.

Remarks.—*D. cuitecensis* belongs to the *zimmermani* group of Mutuura and Munroe (1972).

Figs. 2–4. *Dioryctria cuitecensis*. 2, Male genitalia (most of left valva and aedeagus omitted). 3, Aedeagus. 4, Ductus bursae and corpus bursae of female genitalia. Scale lines = 1.0 mm.

Key to Mexican Species of *Dioryctria*

1. Forewing without raised scales 2
– Forewing with raised scales 5
2. Forewing with many red or orange scales; valva with distal part blunt and short, at most slightly falcate; ductus bursae with sclerotized part usually shorter than length of corpus bursae 3
– Forewing with only few red or orange scales; valva with distal part distinctly produced apically; ductus bursae with sclerotized part about as long as, or longer than, length of corpus bursae 4
3. Forewing with obvious antemedial line . . . . *auranticella* (Grote)
– Forewing without antemedial line . . *rossi* Munroe
4. Forewing heavily dusted with white (moth appearing mostly gray); male antenna weakly serrate . . . . *pinicolella* Amsel
– Forewing lightly dusted with white (moth appearing mostly brown or fuscous); male antenna strongly serrate (appearing almost unipectinate) . . . . *majorella* Dyar

5. Uncus constricted at base with distinct lateral protuberances; ductus bursae with proximal part distinctly narrower than distal part .. 6
– Uncus not constricted at base and without lateral protuberances; ductus bursae with proximal part about as wide as, or wider than, distal part 9
6. Valva with dorsal part broad distally (about 4× as wide as more setiferous ventral part); ductus bursae with distal end simple, well separated from proximal spines of corpus bursae 7
– Valva with dorsal part more narrow distally (about 2–2.5× as wide as more setiferous ventral part); ductus bursae with distal end with attached sclerite supporting proximal spines of corpus bursae 8
7. Forewing mostly reddish brown; valva with distal part wide and blunt; ductus bursae with sclerotized part about as long as corpus bursae ..... *erythropasa* (Dyar)
– Forewing with few reddish brown scales; valva with distal part produced into a slender curved hook; ductus bursae with sclerotized part longer than corpus bursae .. .. *martini* Mutuura and Neunzig
8. Forewing gray, densely dusted with white and with distinct transverse lines ..... *albovittella* (Hulst)
– Forewing brown, with only very few scales dusted with white and without distinct transverse lines (Fig. 1) .. ... *cuitecensis* Neunzig
9. Forewing with narrow, interrupted, black longitudinal line extending most of length of wing (starts near base at CuA_1 and extends through discocellular area); valva with dorsal projection extending well beyond apex of ventral part of valva ... *cibriani* Mutuura and Neunzig
– Forewing without black longitudinal line extending most of length of wing; valva with dorsal projection barely exceeding apex of ventral part of valva 10
10. Forewing ground color pale gray and with strongly contrasting black subbasal scale ridge, black outer border of antemedial line, black inner border of postmedial line, and small black scale ridge following antemedial line; ductus bursae with proximal part bulbous .. .. *subtracta* Heinrich
– Forewing ground color brown, without black strongly contrasting scales associated with scale ridges and transverse lines; ductus bursae with proximal part not strongly expanded .... *durangoensis* Mutuura and Neunzig

Acknowledgments

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FINE STRUCTURE OF THE EGGS OF *PSOROPHORA COLUMBIAE, PS. CINGULATA* AND *PS. FEROX* (DIPTERA: CULICIDAE)

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Abstract.—The eggs of *Psorophora columbiae, Ps. cingulata* and *Ps. ferox* are described with reference to scanning electron micrographs. In contrast to earlier descriptions, complete details of the *Ps. columbiae* and *Ps. ferox* eggs are given, including the anterior end and micropyle, posterior end, and intact outer chorion. This is the first account of the egg of *Ps. cingulata*. Eggs of *Ps. ferox* from Florida are discernibly different from a Trinidad population in terms of the number and form of the small outer chorionic tubercles in each chorionic cell.

Key Words: Insecta, mosquito, egg, fine structure, chorionic structure

The known distribution of *Psorophora (Grabhamia) cingulata* (Fab.) extends through Trinidad, possibly Central America and much of South America (Knight and Stone 1977). It is a species about which little is known, except for a number of records of the larval habitat (Heinemann et al. 1980). Its egg is described here for the first time.

Psorophora (Janthinosoma) ferox (von Humboldt) is a very widespread species, ranging from South through Central America, the Greater and Lesser Antilles, the eastern United States and south-eastern Canada. The egg of this species was first described by Horsfall et al. (1952), from eggs stripped of the outer chorion. Subsequently, using eggs prepared in the same way, Horsfall et al. (1970) published scanning electron micrographs showing the inner chorionic sculpturing. Although eggs lacking the outer chorion are adequate to demonstrate the basic outline pattern of the outer chorionic cells, the entire structural detail of the outer chorion is lost. In this paper we provide the first description of the intact egg, including details of the posterior end and anterior end and micropyle. The description is based on eggs from *Ps. ferox* collected in Florida, but we also describe and illustrate differences in eggs from a Trinidad population.

In their papers cited above, Horsfall and associates described (as *Ps. confinnis*) the egg of *Ps. (Grabhamia) columbiae* (Dyar and Knab). Their material was collected from the eastern United States, which would imply that it is *Ps. columbiae* as currently recognized (Belkin et al. 1970, Darsie and Ward 1981). Bosworth et al. (1983) examined *Ps. columbiae* eggs in more detail as part of their study of eggs of the *Ps. confinnis* complex from 7 areas of the country. However, as in the work by Horsfall and co-workers, the outer chorion was first removed, then the sculpturing of the inner chorion in the anterolateral part of the egg was compared by scanning electron microscopy (SEM). None of these studies, therefore, has presented a description of the egg in its natural form (outer chorion intact), or of all its parts. Following the more complete account in this

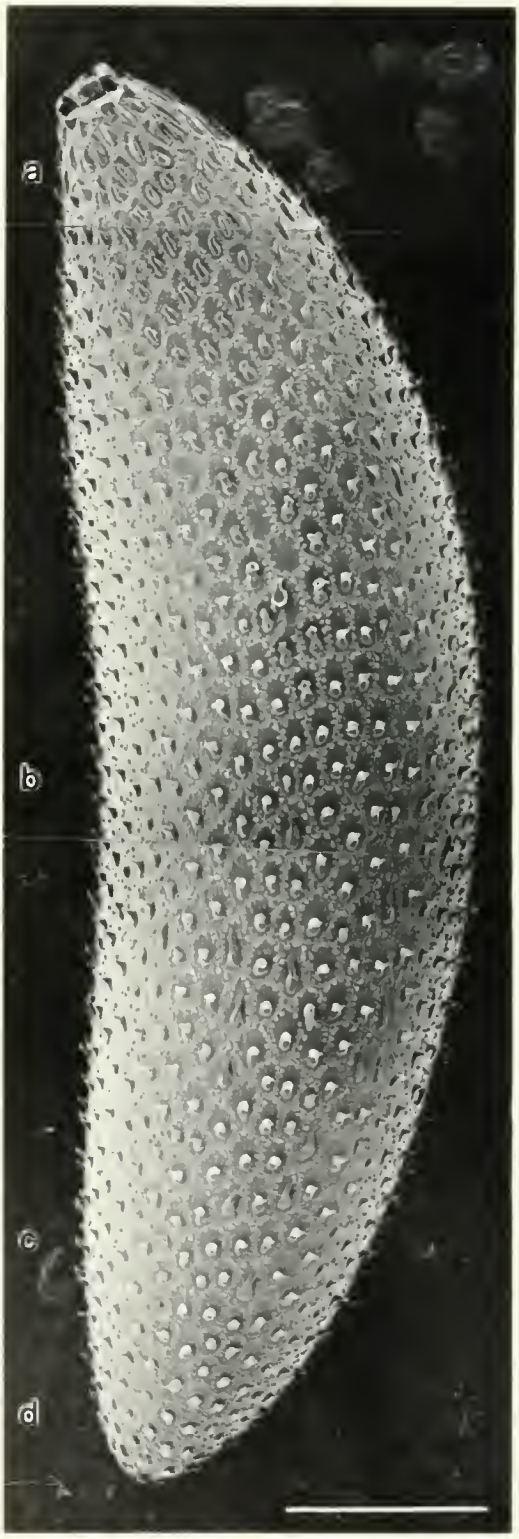

Fig. 1. *Ps. columbiae.* Entire egg, anterior end uppermost. Scale = 100 μm.

paper, we point out some characters of the intact egg that may be of value in evaluating a species complex.

Materials and Methods

Eggs of *Ps. cingulata* and of *Ps. ferox* were obtained from females collected in the vicinity of Arena, Trinidad, blood-fed and then induced to oviposit in the laboratory. Eggs were allowed to embryonate and were then preserved in 30% ethanol, pre-filtered through a 0.45 μm polycarbonate membrane, and sent to Vero Beach. On arrival, the eggs were pipetted onto small circles of filter paper and air-dried.

Psorophora ferox eggs from Vero Beach were obtained from females collected on the grounds of the Florida Medical Entomology Laboratory. Eggs of *Ps. columbiae* were from a small laboratory colony established from material collected within a few miles of Vero Beach. When fully embryonated, eggs of both species were suspended in cold, filtered water long enough to pipette them onto circles of filter paper, where they were air-dried. For all three species the paper circles were then attached to stubs with silver paint, completely desiccated over calcium chloride, then coated with gold. Specimens were examined in a Hitachi S-510 SEM.

Measurements of living eggs were done with a stereomicroscope and ocular micrometer. Dimensions and ranges of structures on the egg surfaces were determined from inspection of 5 eggs in each case. The terminology follows Harbach and Knight (1980), except for the terms "anterior ring" and "outer chorionic cell field," defined by Linley (1989).

Results

Psorophora (*Grabhamia*) *columbiae* (Figs. 1–3)

Size: dimensions as in Table 1.

Color: dull black.

Overall appearance: broadly banana-shaped, dorsal curvature greater than ventral, widest at about anterior ⅓, posterior portion gradually tapered, anterior taper

Table 1. Dimensions of eggs of three species of *Psorophora* (n = 10).

Species	Length μm		Width μm		L/W ratio	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Ps. columbiae	860.9 ± 17.8	736.4–936.4	235.5 ± 3.4	218.2–254.5	3.66 ± 0.05	3.24–3.81
Ps. cingulata	762.1 ± 1.8	749.9–766.6	240.1 ± 1.8	233.3–249.9	3.18 ± 0.03	2.99–3.29
Ps. ferox (Fl)	904.5 ± 13.7	845.5–963.6	250.2 ± 3.6	227.9–265.5	3.62 ± 0.03	3.44–3.75
Ps. ferox (Tr.)	918.3 ± 1.9	911.0–927.7	316.7 ± 1.7	311.1–322.2	2.90 ± 0.02	2.83–3.04

more abrupt and pointed, overall surface appearing spiny, micropylar collar distinct (Fig. 1). Outer chorionic cells longitudinally elongated, each with many small peripheral tubercles and a single large, elongate, anteriorly inclined tubercle (Fig. 1).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 1). Chorionic cell structure typified by mid-lateral cells, middle of egg, as follows. Shape mostly hexagonal, occasionally pentagonal, outlines quite variable (Fig. 2e), length 17–26 μm, width 11–18 μm. Cell fields about 2 μm smaller in each dimension. Each cell with a single, large, elongate, anteriorly inclined tubercle, positioned towards posterior part of cell, and a variable number of small tubercles around cell periphery (Figs. 2e, 3e; Table 2). Size distribution (largest diameter) of small tubercles bimodal (Fig. 4), size increase highly significant from posterior to anterior part of cell (Fig. 5). Each large tubercle consisting of a distinct base, upper part of tubercle smooth (but see variations, below), often inclined upward only in anterior ½, length 7–12 μm, width 3–5 μm. Cell floor covered with tiny, more or less round tubercles (Fig. 3e), diameter 0.1–0.2 μm, fewer posterior to large tubercle. Small tubercles tending to be oval, with flared base and distinct upper portion, entire tubercle slightly elongated in same axis as adjacent outer chorionic reticulum (Fig. 3e, f). Chorionic reticulum a fine meshwork, width 1.9–2.7 μm, with central line of closely spaced or fused bead-like protuberances, diameter 0.3–0.6 μm (Fig. 3f).

Outer chorionic cell structure differs from anterior to posterior part of egg. Outer chorionic cells close to anterior end smaller, length 16–21 μm, width 9–13 μm, large tubercles flat or not as erect, often pointed, with rough upper surfaces (Fig. 3a), small tubercles more irregular. At middle of egg large tubercles more tongue-shaped, almost always erect, smooth, small tubercles more regular (Fig. 3b). Approaching posterior end chorionic cells smaller, length 15–19 μm, width 13–19 μm, large tubercles smaller (Fig. 3c). Cells very close to posterior end even smaller, large tubercles much shorter, cap-like, small tubercles fewer (Fig. 3d).

Anterior end, micropyle: outer chorionic cells as described (Fig. 3a), anterior ring present, diameter 41–44 μm, width 3–9 μm, outer margin with anteriorly curved points (Fig. 2a). Micropylar collar very distinct, almost always complete (no gaps), flared anteriorly (Fig. 2a), height 11–12 μm, outer diameter about 26 μm, outer margin irregular (Fig. 2b, c), wall width variable, 1.5–8 μm, inner diameter about 14 μm, inner edge slightly irregular (Fig. 2c). No micropylar disc visible, micropyle diameter about 2.5 μm.

Posterior end: outer chorionic cells close to end as described (Fig. 3d), end rounded, large tubercles in cells button-like (Fig. 2d).

Psorophora (*Grabhamia*) *cingulata* (Figs. 6–8)

Size: dimensions as in Table 1.

Color: dull black.

Overall appearance: broadly cigar-shaped, dorsal curvature greater than ventral, anterior end somewhat conical, posterior more rounded, surface somewhat spiny but less so than *Ps. columbiae,* micropylar collar sometimes fairly distinct (Fig. 6), but often not so (Fig. 7a). Outer chorionic cells as in

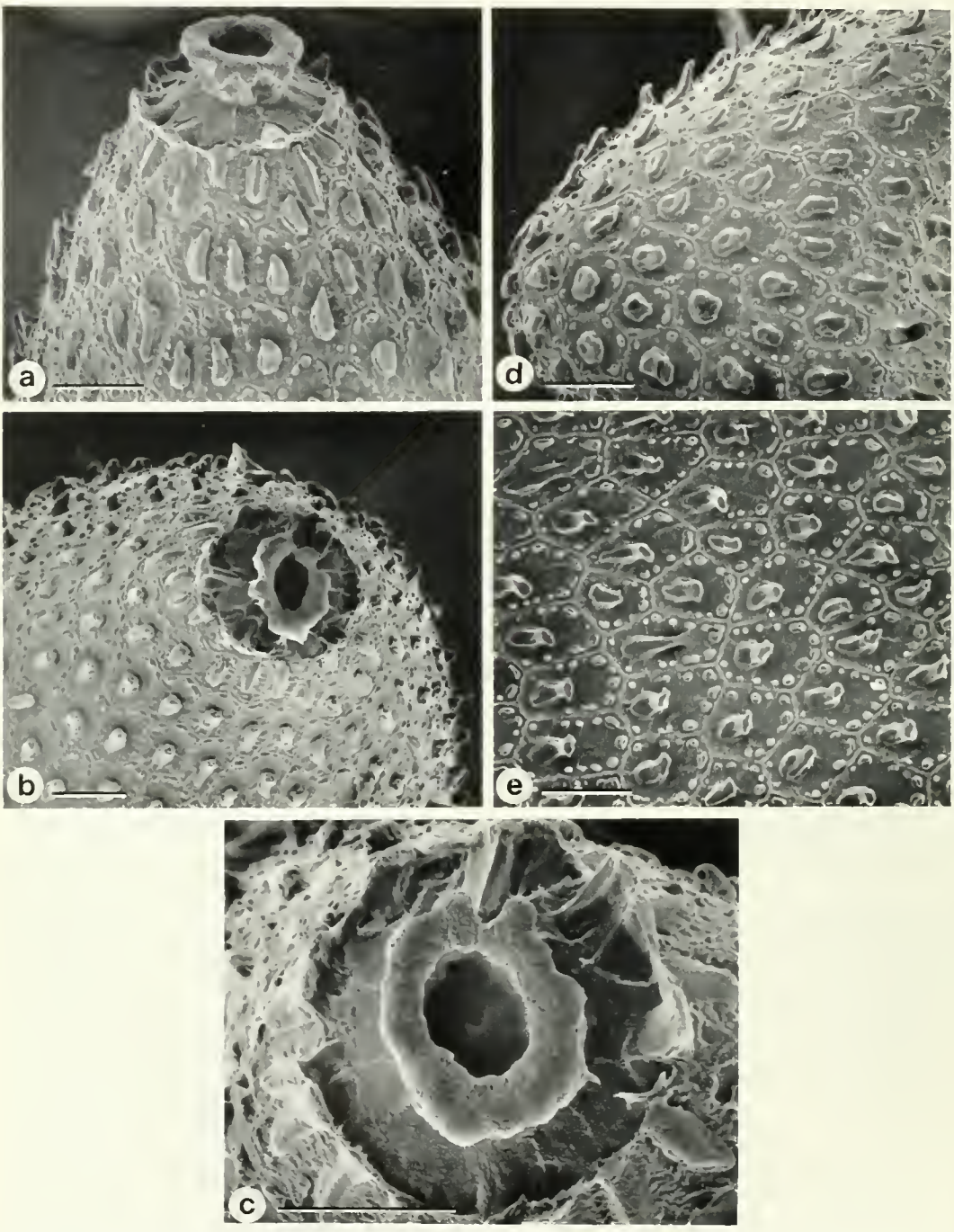

Fig. 2. *Ps. columbiae*. (a) anterior end, dorsal surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells, lateral surface, middle of egg. Scale = 20 μm.

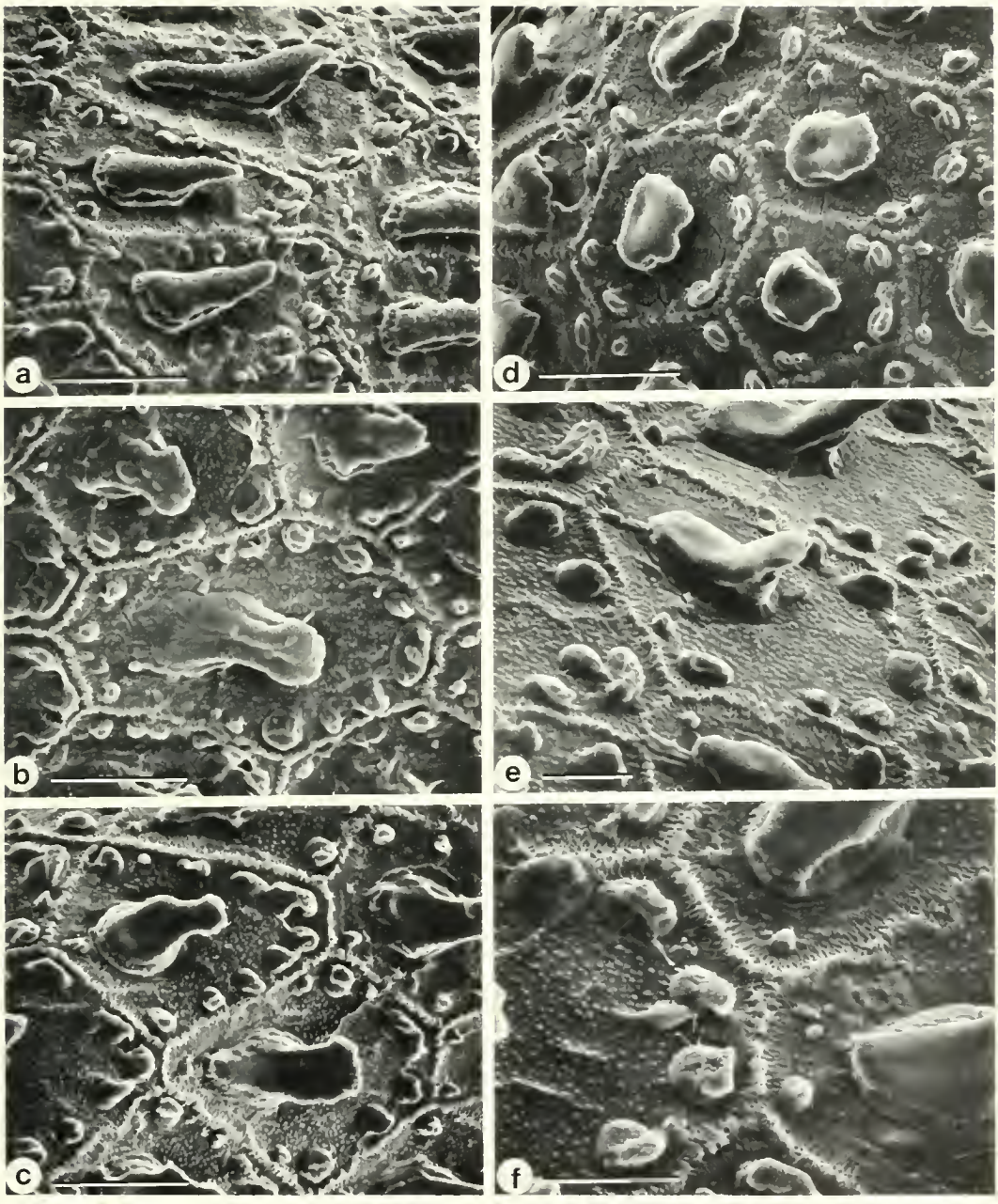

Fig. 3. *Ps. columbiae*, details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 1). (a) close to anterior end; (b) at about anterior ⅓; (c) at about posterior ⅓; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = 10 μm (a, b, c, d, e), = 5 μm (f).

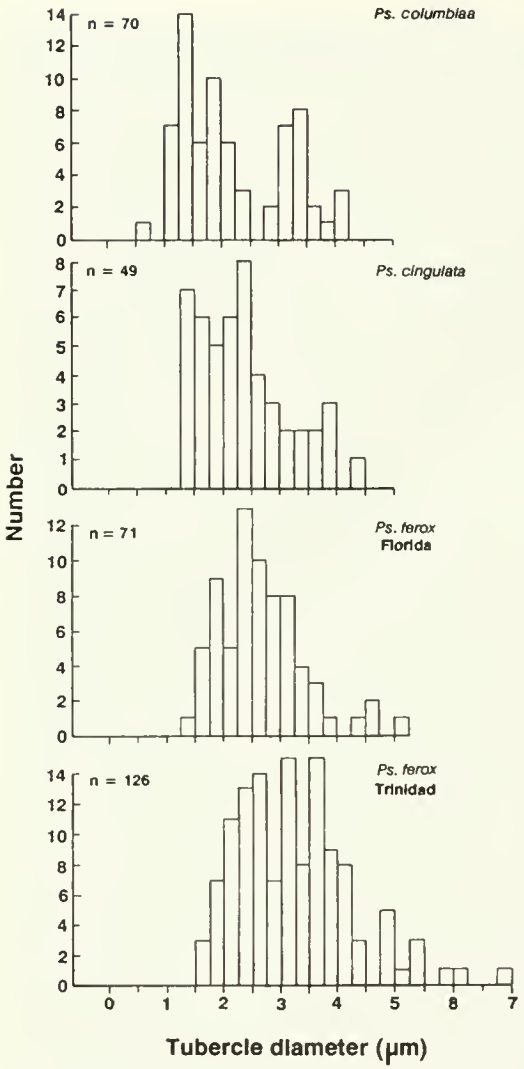

Fig. 4. Size distributions of small outer chorionic tubercles.

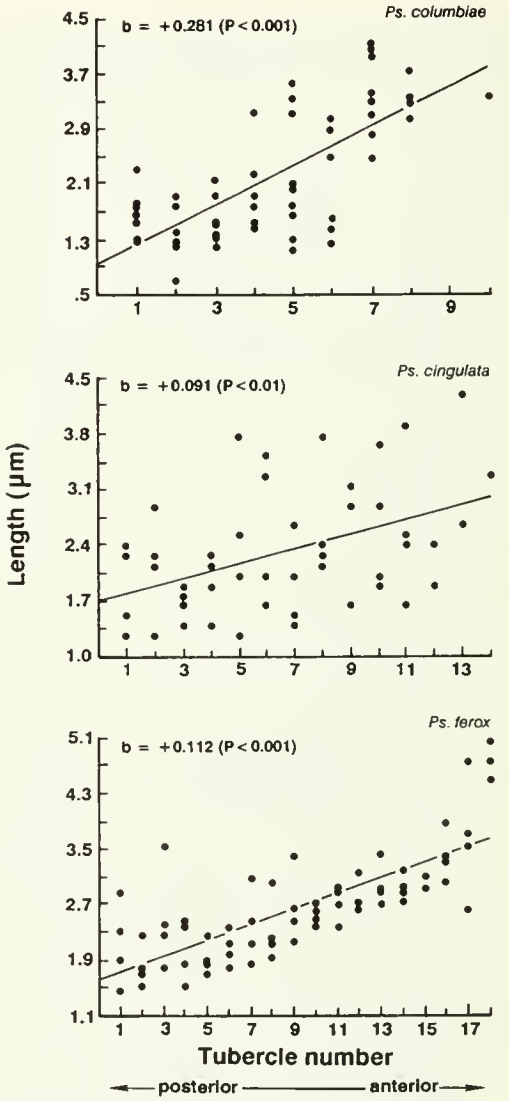

Fig. 5. Regressions of small tubercle length (largest dimension) on position in outer chorionic cell (number of tubercle indicates its numerical position relative to posterior cell boundary).

Ps. columbiae except that small, peripheral tubercles more numerous (Table 2) and large tubercle sometimes anteriorly inclined, sometimes decumbent (Fig. 6).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 6). Outer chorionic cells usually hexagonal, occasionally pentagonal, outlines variable (Fig. 7e), length 25–43 μm, width 21–25 μm. Cell fields about 2 μm smaller in each dimension. Single large tubercle positioned well towards posterior part of cell, often inclined anteriorly, but often flat, owing to attachment to cell floor at anterior end (Fig. 7e). Small tubercles variable in number (Table 2), size distribution (largest diameter) skewed (Fig. 4), size increasing significantly from poste-

Table 2. Numbers of small outer chorionic tubercles in three species of *Psorophora*.

Species	n	Number of small tubercles*	
		Mean ± SE	Range
Ps. columbiae	49	11.9 ± 0.3	7–16
Ps. cingulata	31	25.0 ± 0.4	20–29
Ps. ferox (FL)	36	32.9 ± 1.7	17–51
Ps. ferox (Tr.)	28	27.5 ± 0.6	23–35

* In outer chorionic cells, mid-lateral surface, middle of egg.

rior to anterior part of cell, but this progression not as great as in *Ps. columbiae* (Fig. 5) and not easily discerned in individual cells (Figs. 7e, 8b). Base of attachment of large tubercle fairly small, upper surface (Fig. 8e) fissured at base, at anterior end, and around edge, smoother centrally (but see variations, below), length 8–18 μm, width 5–7 μm. Cell floor with many tiny, round tubercles (Fig. 8e), diameter 0.1–0.5 μm. Small peripheral tubercles irregular in shape, longest dimension tending to parallel adjacent chorionic reticulum (Fig. 8b), each tubercle having a flared base and distinct upper portion, surfaces smooth (Fig. 8e, f). Outer chorionic reticulum a fine meshwork, only slightly raised, width 0.7–1.5 μm, with central line of closely spaced or intermittently fused bead-like protuberances, diameter 0.3–0.4 μm (Fig. 8f).

Variations in outer chorionic cell structure as follows. Cells close to anterior end smaller, length 22–28 μm, width 12–16 μm, large tubercles usually flat or very little erect (Figs. 7a, 8a), more pointed, length 8–17 μm, width 4.5–6.5 μm, upper surfaces entirely rough (Fig. 8a). Small tubercles more irregular. Approaching posterior end outer chorionic cells become somewhat smaller, length 21–35 μm, width 17–20 μm. Large tubercles longer (9–21 μm), almost always decumbent (Fig. 7d), attached anteriorly to cell floor, often by ragged, finger-like extensions (Figs. 7d, 8c), surfaces smooth except for anterior edges (Fig. 8c). Immediately at

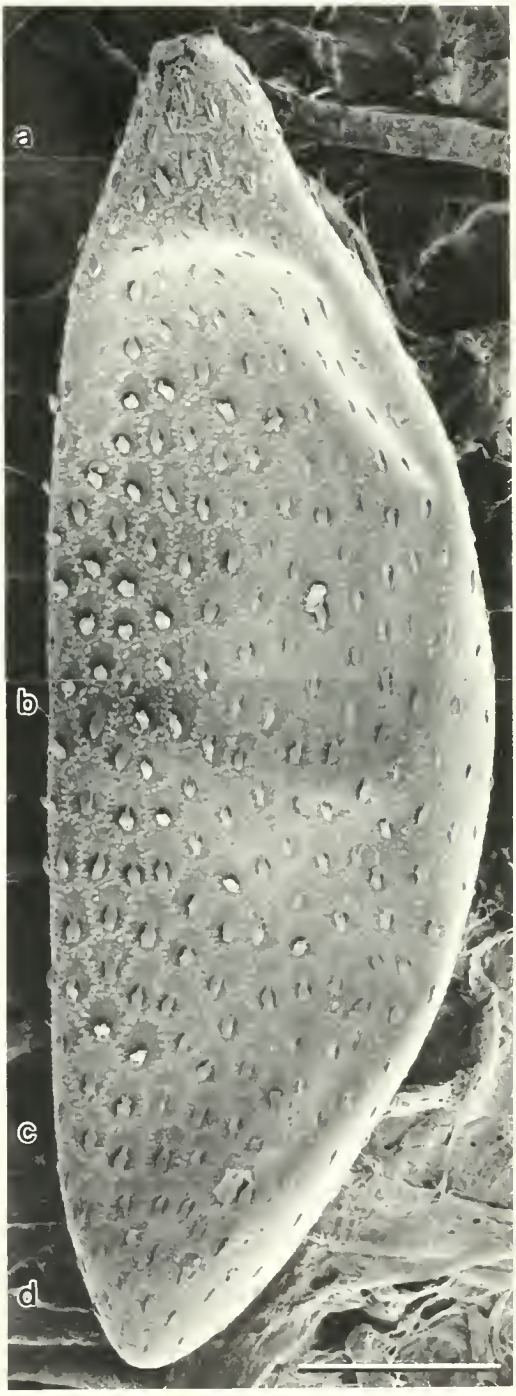

Fig. 6. *Ps. cingulata*. Entire egg, anterior end uppermost. Scale = 100 μm.

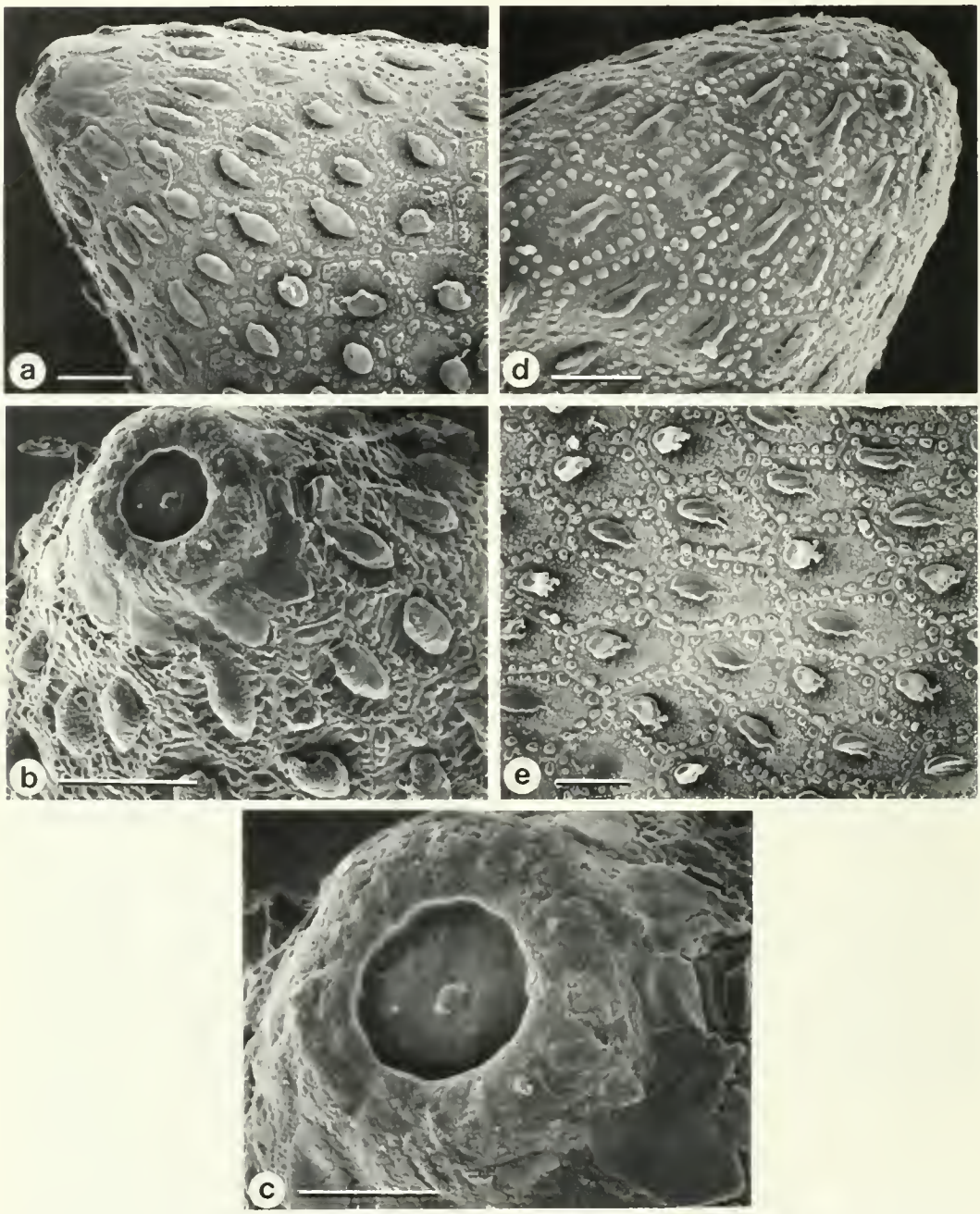

Fig. 7. *Ps. cingulata.* (a) anterior end, dorsal surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells, lateral surface, middle of egg. Scale = 20 μm (a, b, d, e), = 10 μm (c).

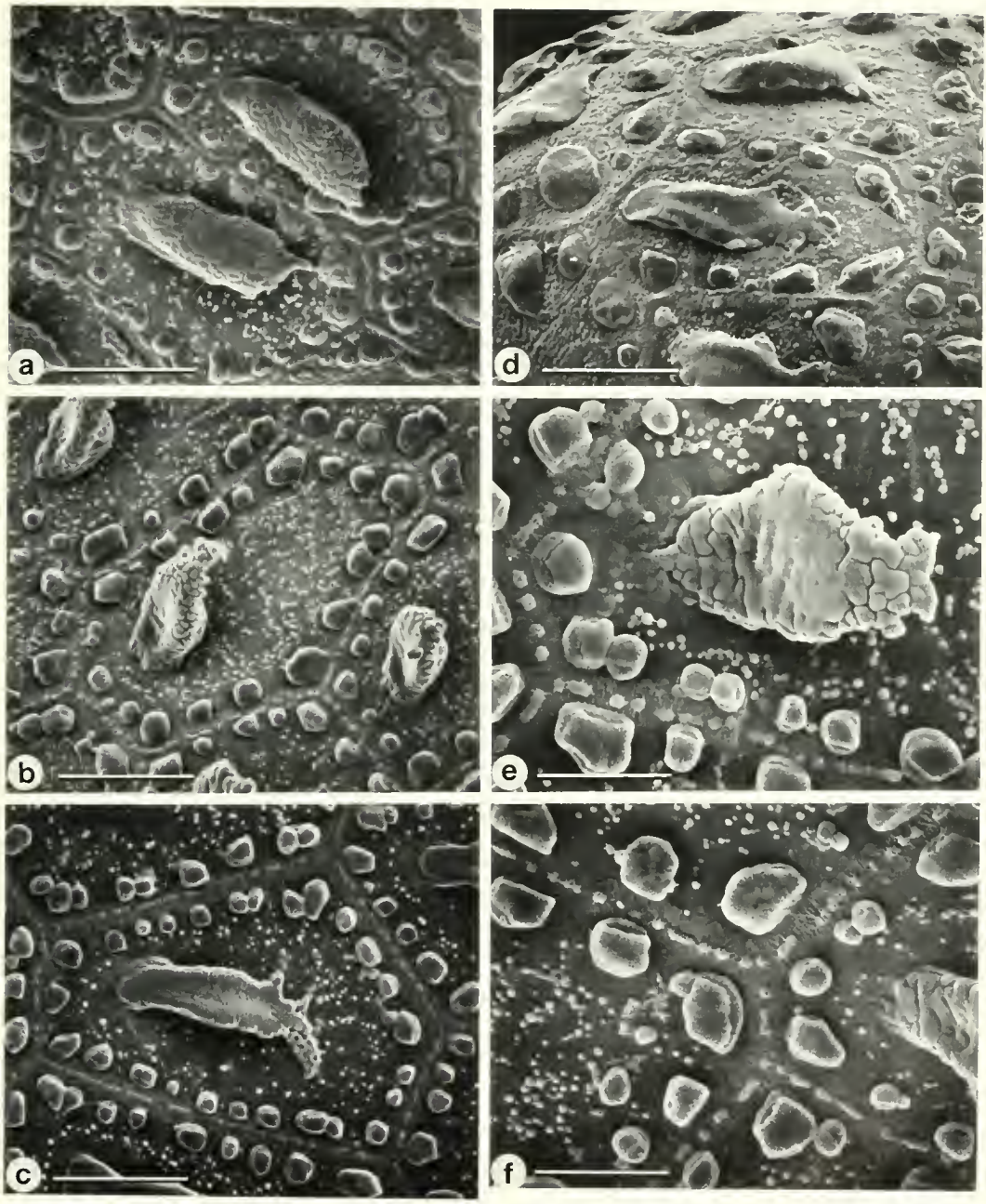

Fig. 8. *Ps. cingulata,* details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 6). (a) very close to anterior end; (b) at about anterior ⅓; (c) at about posterior ⅓; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = 10 μm (a, b, c, d), = 5 μm (e, f).

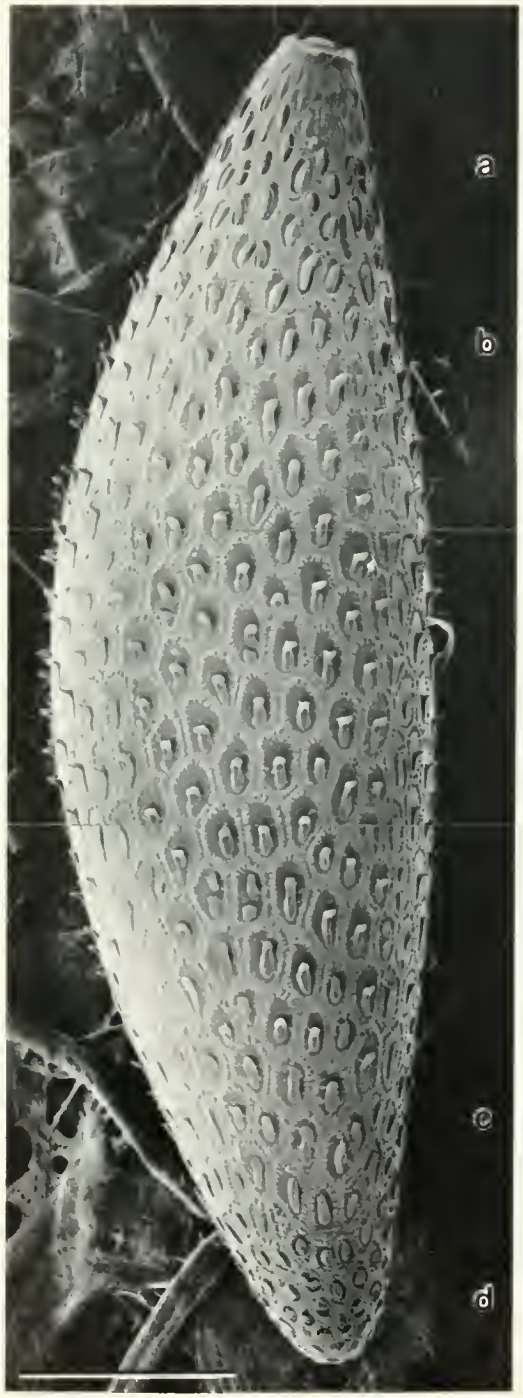

Fig. 9. *Ps. ferox.* Entire egg, anterior end uppermost. Scale = 100 μm.

posterior end large tubercles become scale-like, appressed to cell floors, anterior margins ragged, surfaces smooth (Fig. 8d). Small tubercles few in number.

Anterior end, micropyle: outer chorionic cells as described (Figs. 7a, 8a). Anterior ring absent. Micropylar collar sometimes fairly distinct (Fig. 6), but usually not so (Fig. 7a), complete, height 8–10 μm, usually tapered, outer diameter about 27 μm, outer margin quite regular, but surface rough (Fig. 7b, c), wall width fairly uniform, 5.2–7 μm, inner collar diameter about 13 μm, inner edge formed of a ring of very shallow excavations (Fig. 7b, c). Micropylar disc not clearly visible, micropyle diameter about 2.2 μm.

Posterior end: outer chorionic cells as described, pole rounded, large tubercles in cells capping end button-like (Fig. 7d).

Psorophora (*Janthinosoma*) *ferox*
(Figs. 9–11)

Size: dimensions as in Table 1.

Color: black.

Overall appearance: shape somewhat to quite fusiform, dorsal curvature greater than ventral, width greatest just anterior to middle, anterior end especially conical, surface spiny, micropylar collar rather inconspicuous (Fig. 9). Outer chorionic cells distinct, longitudinally elongated, with many peripheral small tubercles and one long, anteriorly inclined one (Fig. 9).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 9). Chorionic cells almost always hexagonal, occasionally pentagonal (Fig. 10e), quite uniform in shape (Fig. 8), length 27–43 μm, width 17–24 μm. Cell fields about 2 μm less in each dimension. Each cell with single very long, tongue-like tubercle originating very close to posterior margin of cell field and extending to about anterior ⅓ (Fig. 10e), tubercle much more sharply inclined from about anterior ⅓ (Fig. 10e). Small peripheral tubercles numerous (Figs. 10e, 11b, e)

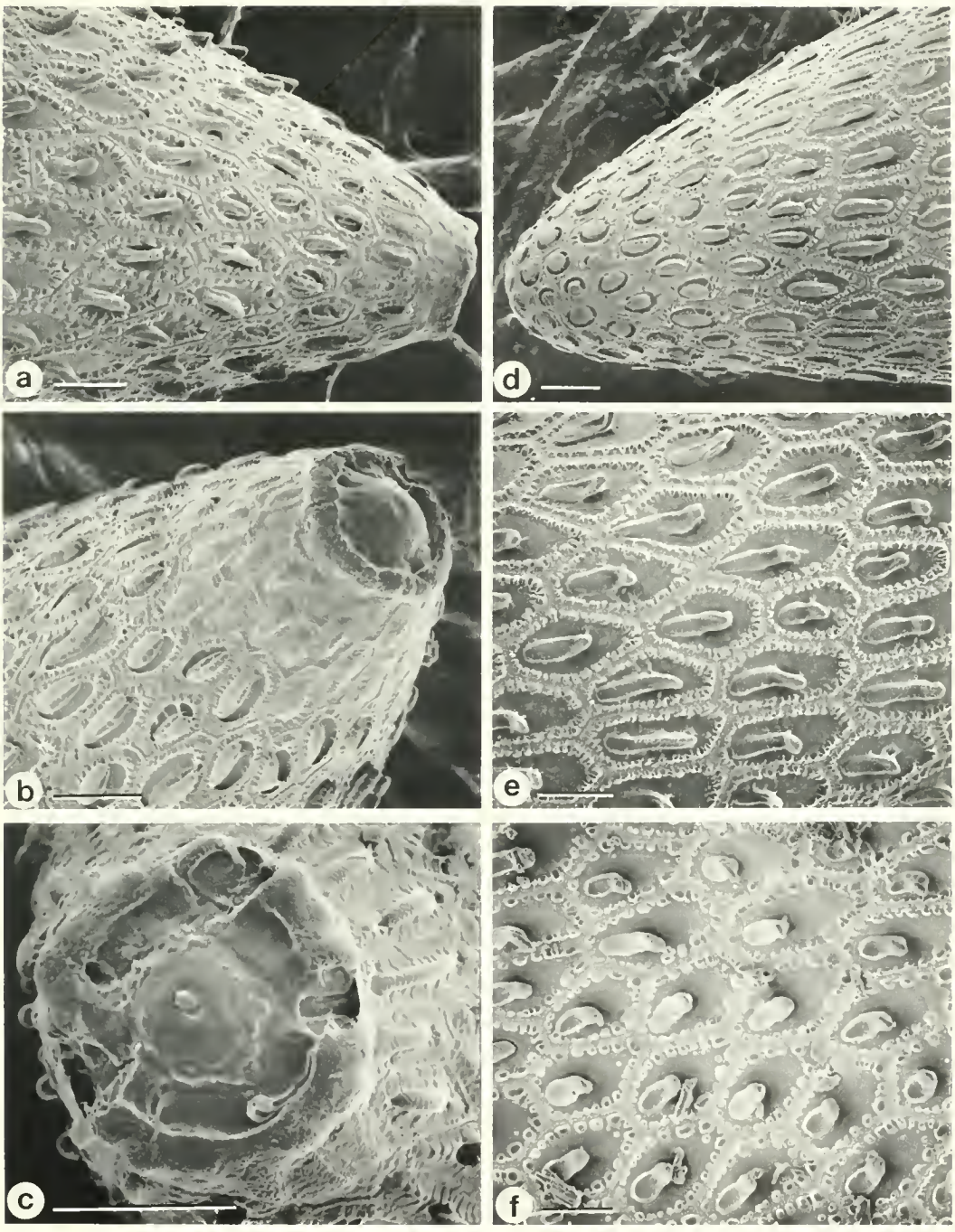

Fig. 10. *Ps. ferox*. (a) anterior end, lateral surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells (Florida), lateral surface, middle of egg; (f) typical outer chorionic cells (Trinidad), lateral surface, middle of egg. Scale = 20 μm.

and numbers variable (Table 2), longest dimension usually perpendicular to adjacent chorionic reticulum, size distribution skewed (Fig. 4), and size increasing highly significantly from posterior to anterior part of cell (Fig. 5), as easily visible (Fig. 10e). In detail, large tubercles made up of distinct, flared base, with rough sides (Fig. 11e), supporting tongue-shaped upper portion. Length of tubercle 13–25 μm, width 5.5–7 μm, surface covered with irregular bumps, slightly more defined anteriorly, less so posteriorly (Fig. 11e). Cell floor covered with many tiny tubercles (Fig. 11e, f), diameter 0.1–0.4 μm, tending to be more numerous anteriorly. Small tubercles irregular, but usually tending to be rectangular (Fig. 11b, f), with widely flared base and small, caplike upper portion, surfaces smooth (Fig. 11f). Chorionic reticulum an intricate, fine meshwork, slightly raised, width 1.1–2.2 μm, with a double, centrally positioned row of small protuberances, diameter 0.1–0.4 μm (Fig. 11e, f). Meshwork of reticulum often extending up outer sides of small tubercles (Fig. 11f).

Structural differences in chorionic cells as follows. Close to anterior end cells considerably smaller, length 16–24 μm, width 9–14 μm. Cell fields become progressively smaller (Fig. 10a, b) until only partially open, usually along one side of large tubercle (Fig. 11b). Inner margins of small tubercles eventually fuse with large tubercle, forming continuous layer (Figs. 10a, b, 11a). Large tubercles not as steeply inclined, becoming more decumbent (Fig. 10a), small tubercles becoming lower anteriorly, shape more irregular, bases flatter, caps often with bumpy surfaces (Fig. 11a). Immediately behind anterior end small tubercles almost disappear (Figs. 10b, 11a), large tubercles appearing as low humps on cell surface (Fig. 10b). Meshwork of chorionic reticulum not distinct, the two central rows of small protuberances closer, forming prominent ridge (Fig. 11a). Somewhat further from anterior end cells much more as in middle of egg, but large tubercles not as steeply inclined (Fig. 11b), meshwork of reticulum visible but not as distinct, and its two central rows not as widely separated. Towards posterior end, progressive changes are similar to those at anterior end (Figs. 9, 10d). Cells become smaller, small tubercles flatter, large tubercles completely decumbent (Figs. 10d, 11c). Cells at posterior end have partially or almost completely occluded fields, very indistinct or almost indistinguishable small tubercles, and reticulum with meshwork scarcely detectable and pronounced central ridge (Fig. 11d). Large tubercles button-like with surface sculpturing less distinct (Figs. 10d, 11d) and almost invisible on most posterior ones (Fig. 11d).

Anterior end, micropyle: chorionic cells as described. Anterior ring absent, micropylar collar visible but not prominent (Fig. 10a, b), not complete (gaps present), height 7 μm, outer diameter about 40 μm, outer margin bumpy (Fig. 10b, c), wall width variable, 0–6 μm, inner collar diameter about 27 μm, inner margin quite smooth, with very shallow excavations (Fig. 10b, c). Micropylar disc very prominently domed (Fig. 10b, c), diameter about 14 μm, micropyle diameter about 2 μm.

Posterior end: outer chorionic cells as described, rather conical, tapering, and end smoothly rounded (Fig. 10d).

Examination of eggs of *Ps. ferox* from Trinidad revealed a number of distinct differences from the Florida population. Although Trinidad eggs were longer (Table 1), they were not significantly so (*t*-test). They were, however, significantly greater in width ($P < 0.001$), and the length/width ratio consequently was smaller ($P < 0.001$). The outer chorionic cells were similar in outline appearance, but differences in the small peripheral tubercles rendered the Trinidad eggs visually distinct (Fig. 10f cf. 10c). The mean number of tubercles per cell in Trinidad eggs was significantly ($P < 0.01$) smaller (Table 2), and their size, on average, clearly greater (Fig. 4). Normalization by logarithmic

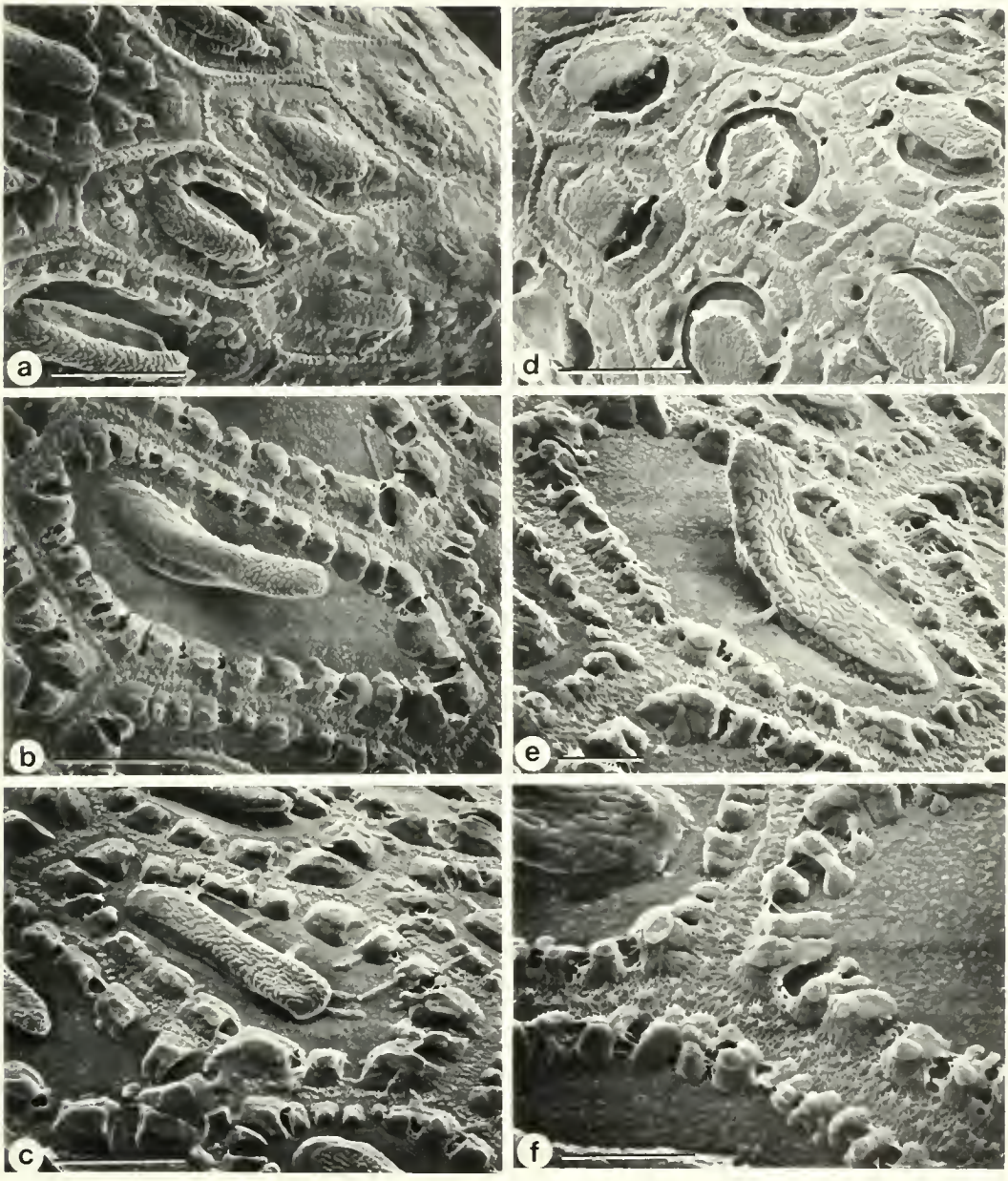

Fig. 11. *Ps. ferox*, details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 9). (a) very close to anterior end; (b) at about interior ⅓; (c) at about posterior ¼; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = 10 μm (a, b, c, d), = 5 μm (e, f).

transformation of the size distributions indeed proved the tubercles of Trinidad eggs to be larger ($P < 0.001$), as easily discernible in the micrographs (Fig. 10f cf. 10e). In addition to this difference in terms of their largest dimension, the shape of the small tubercles also was different. Thirty tubercles (10 randomly picked from each of 3 eggs

for each population) were measured to record their radial (relative to the cell) and circumferential diameters and the ratios (r/c) calculated. The mean (±SE) Trinidad ratio (1.02 ± 0.03) was significantly ($P < 0.001$) smaller than the Florida sample (1.53 ± 0.06), implying a much closer approximation to square in the Trinidad eggs (Fig. 10f cf. 10e).

Discussion

In their survey of the morphology of the inner chorion of eggs of the *Ps. confinnis* complex, Bosworth et al. (1983) examined 21 eggs of *Ps. columbiae* from the same location (Indian River County) as the material studied here. Their inner chorionic pattern type B was the most frequent (67%), with types A (5%), D (14%) and G (14%) also present. Type B is generally consistent with the intact eggs we examined. Notches in the cell outline (corresponding to the midline of the outer chorionic reticulum), some with short ridges extending into the cell field, are visible in Fig. 2e. Some cells seen at higher magnification also accord with type B (Fig. 3a, c, f) in that they appear to have short ridges in the cell fields, not connected with the reticulum. Type D as described by Bosworth et al. (1983) is similar to Type B, except that the cells contain a "cellular disc," which obviously represents an impression of the base of the cell's large tubercle on the inner chorion. Why only some cells stripped of the outer chorion show this impression is not clear. It has occurred to us, however, that the presence or absence of an impression could be determined by inconsistencies in preparative technique. These eggs were rolled on sticky tape to remove the outer chorion (Bosworth et al. 1983) and presumably were subjected to at least some pressure. Differences in this pressure could have caused a gradation in the amount of detail impressed onto the inner chorion. Outer chorionic structures are easily removed from these eggs by abrasion. Thus, it is also possible that some or many of the cells lacked the outer chorionic tubercles when the egg was applied to the sticky tape and could not have left an impression. Admittedly, cell outlines are not likely to be affected by removal of the outer chorion, but the possibility of preparative artifacts suggests the need for caution when interpreting inner chorionic patterns.

Given that egg surfaces are to be examined by SEM, there is nothing to be gained by removing the outer chorion. Aside from possible artifacts, much structure, along with its potential variation, is lost. This is illustrated by *Ps. ferox* eggs from Trinidad and Florida, where the number, greatest diameter and form of the small tubercles were all demonstrably different. The small tubercles were, of course, removed from eggs studied by Bosworth et al. (1983), but there is suggestive evidence that they may differ in number between populations of the *Ps. confinnis* complex. A few of the eggs from Arkansas and Texas possessed an unusual inner chorionic pattern (type J), in which the periphery of each cell was lined with small ovoid pits, almost certainly corresponding to the small tubercles. Bosworth et al. (1983) state that 15–20 pits were present in each cell, apparently more than in *Ps. columbiae* eggs from Florida, where the numbers ranged from 7–16 (mean 11.9) in 49 cells counted. Tubercle numbers are related to cell size, but the anterolateral cells studied by Bosworth and co-workers would tend to be smaller (and therefore have fewer tubercles) than those selected here, which were laterally positioned in the middle of the egg. A re-examination of eggs of the *Ps. confinnis* complex, making use of the intact structural detail of the outer chorion, should be undertaken.

Acknowledgments

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RESOURCE UTILIZATION BY LARVAE OF *PARACANTHA GENTILIS* (DIPTERA: TEPHRITIDAE) IN CAPITULA OF *CIRSIUM CALIFORNICUM* AND *C. PROTEANUM* (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—Resource utilization and resource sharing by larvae of *Paracantha gentilis* Hering were analyzed in capitula of two native thistles (Tribe Cynareae): *Cirsium californicum* Gray and *Cirsium proteanum* J. T. Howell. Guilds described and analyzed for thistle-insect systems in Europe, though more complex than in southern California, apparently lack phytophages with the trophic strategy of *P. gentilis*. This tephritid displays rarely solitary, mainly aggregated attack on immature, closed capitula, but unlike European Tephritidae, does not form galls or otherwise cause host-tissue proliferation. Instead, feeding behavior of third instars of *P. gentilis* showed a density-dependent change in feeding niche from ovule-feeding alone to ovule, upper receptacle and plant-sap feeding which extended the range of available resources and minimized intraspecific competition.

The feeding-niche of *P. gentilis* in thistle capitula is novel by European criteria, and exemplifies the failure of phytophage communities to converge in structure despite similar resources on different continents.

Key Words: Insecta, resource utilization, guild structure, Tephritidae, gall-formers, *Cirsium*, evolution, thistles

Resource utilization by thistle-head insects was described by Zwölfer (1985) as ". . . the percent of flower heads in a sample containing phytophagous insects or showing signs of insect damage." This parameter is more precisely measured as the number of damaged achenes per capitulum (= head). Zwölfer (1985) used resource utilization and guild structure to study the feeding ecology of several thistle-insect systems in Europe.

Ten species of *Cirsium* (Asteraceae, Tribe Cynareae) are native to southern California (Munz 1974). Few native stenophagous insect species are associated with native *Cirsium* spp. in North America (Goeden and Ricker 1986a, b, 1987a, b). In contrast, many stenophagous species are associated with European *Cirsium* spp. (Zwölfer 1965). This disparity offers opportunity for comparative studies of resource allocation and resource utilization by thistle-head insects.

Paracantha gentilis feeds in capitula of eight species of native *Cirsium* thistles and the introduced *C. vulgare* (Savi) Tenore in southern California (Goeden and Ricker 1986 a, b, 1987a, b) as well as several different species of native *Cirsium* in northern California (Pemberton et al. 1985) and elsewhere in North America (Steck 1984). In *C. californicum* Gray, Goeden and Ricker (1986b) recorded *P. gentilis* as the dominant phytophage reared from 19 (73%) of 26 samples (average 50 capitula/sample). Three other insect species found in less than 50% of the capitula from the same samples were: *Rotruda mucidella* (Ragonot) (Lepidoptera:

Pyralidae), *Platyptilia carduidactyla* (Riley) (Lepidoptera: Pterophoridae), and *Orellia occidentalis* (Snow) (Tephritidae). *Paracantha gentilis* was reported from 62% of samples of *C. proteanum* capitula by Goeden and Ricker (1986b). Among the three other insect associates mentioned above, *R. mucidella* was the dominant phytophage in *C. proteanum* capitula, occurring in 92% of the samples (Goeden and Ricker 1986b).

Zwölfer (1988) outlined three trophic strategies for thistle capitula-infesting insects in Europe: (1) An early-aggregated attack in closed young capitula, usually combined with gall formation, that lead to gregarious feeding behavior and protection from parasitoids and predators. In Europe, these insect associates are highly host-specific Tephritidae, Cynipidae, and Curculionidae. (2) Feeding on the maturing achenes and receptacle without induction of galls. Oviposition takes place in older capitula, only single eggs are deposited, and capitula already occupied usually are avoided, e.g. Tephritidae and Curculionidae in Europe. (3) Polyphagous species that usually occur singly and oviposit after a capitulum has opened. The larvae are highly mobile, aggressive, often cause accidental mortality of other individuals in a capitulum, and are typically the dominant phytophage, e.g. Anobiidae, Pyralidae, and Tortricidae in Europe. Harris (1989) distinguished between ovule (unfertilized) and soft or hard achene (fertilized ovule)-feeding by insects in knapweed and thistle capitula, a modification of Zwölfer's (1988) scheme which we have used in our discussion.

Preliminary field studies by Goeden and Ricker (1986a, b, 1987a, b) suggested differences from European Tephritidae in the way *P. gentilis* feeds and interacts with other insects infesting capitula of native *Cirsium* thistles in southern California. Comparisons were based on two thistle-insect systems involving (1) a *C. californicum* Gray population in which *P. gentilis* was the only capitulum infesting species and (2) a *C. proteanum* J. T. Howell population in which *P. gentilis* was part of a capitulum-infesting guild composed of as many as four species.

Materials and Methods

Cirsium californicum capitula were sampled at Mill Creek, San Bernardino National Forest, San Bernardino Co., CA, and *C. proteanum* capitula were sampled on Sawmill Mt., Angeles National Forest, Los Angeles Co., CA. Current season's capitula were collected during the Spring and Summer of 1987, 1988 and 1989. Overwintered heads from 1986 were collected in early Spring, 1987, and stored at 5°C for later dissection.

Serial dissections of capitula at different developmental stages were carried out to determine larval feeding behavior. Dissected eggs and larvae were placed in covered glass petri dishes lined with filter paper and soaked with physiological saline and held in darkened growth chambers at 27°C until identified and then were held for pupariation and adult emergence, or were preserved or discarded.

Field sites consisted of scattered individuals and patchy aggregations of 10–50 thistles growing along roads and on south-facing hillsides. At the Mill Creek site, 25 plants were inspected on each sampling date, and a total of 10–25 capitula were collected on each date for later dissection. The number of capitula on all plants occurring in a 3 × 3 m-area at the Mill Creek site was counted on four occasions during April–May, 1988, to determine phenology and capitulum production. Oviposition by overwintered females in the small immature capitula (commonly and erroneously called "buds") also was monitored on a weekly basis for the entire season during 1987 and 1988.

Individual larvae and puparia dissected from capitula were placed in 60-ml^3 plastic vials fitted at one end with 100-mesh brass screening for ventilation and held in the insectary of the Department of Entomology, University of California, Riverside. Insectary conditions were 26° ± 1°C, 30 to 60%

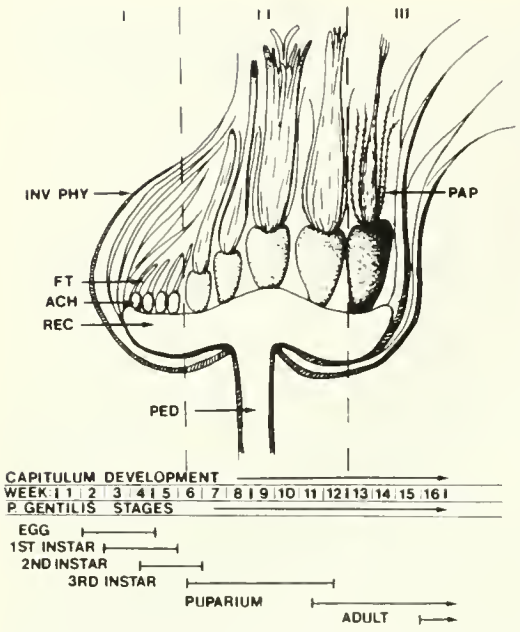

Fig. 1. Phenology of *Paracantha gentilis* in capitula of *C. californicum*. I. Immature capitulum. II. Blossom. III. Post-blossom. ACH, achene; FT, floral tube; INV PHY, involucral phyllaries; PAP, pappus; PED, peduncle; REC, receptacle.

RH, and a 12-12 (l/d) photoperiod. Voucher specimens of all insect species involved are stored in the research collection of RDG, and eventually will be offered to the collection of the Department of Entomology, University of California, Riverside.

Results and Discussion

Resource utilization.—The phenology of *Paracantha gentilis* in capitula of *C. californicum* in southern California is shown in Fig. 1. *Paracantha gentilis* follows the first trophic strategy in Zwölfer's scheme described above, but with a major difference—although it oviposits in closed young capitula and usually feeds gregariously (up to 12 larvae per capitulum), it induces no galls.

In the present study, resource utilization was calculated as the percentage of attacked capitula in a sample (Table 1). The accuracy of this statistic will be discussed below with regard to feeding strategies of capitulum-infesting Tephritidae. Thus, resource utilization by *P. gentilis* in *C. californicum* was 78%, as 153 of 195 capitula examined were attacked. In *C. proteanum* with its complex insect guild, resource utilization by *P. gentilis* was 58% (79 of 134 capitula), by *R. mucidella* was 68% (92 of 134 capitula), and by *O. occidentalis* was 47% (64 of 134 capitula).

Table 1. Resource utilization or percent of *C. californicum* and *C. proteanum* capitula infested by three phytophagous species.[a]

Sample	No. (%) Capitula Dissected	Capitula Attacked P.G	R.M.	O.O.
C. californicum[b]				
1986	15	12 (80%)	0	0
1987	110	86 (78)	0	0
1988	30	24 (80)	0	0
1989	40	31 (77)	0	0
Totals	195	153 (78)	0	0
C. proteanum[c]				
1982[d]	27	18 (66)	20 (74)	21 (78)
1983[d]	27	8 (30)	17 (62)	11 (41)
1986	30	16 (53)	12 (40)	6 (20)
1987	50	37 (74)	43 (86)	26 (52)
Totals	134	79 (58)	92 (68)	64 (47)

[a] P.B., *P. gentilis*; R.M., *R. mucidella*; O.O., *O. occidentalis*.
[b] Mill Creek.
[c] Sawmill Mt.
[d] Unpublished data Goeden and Ricker.

In southern California, *P. gentilis* is an early-aggregated attacker; whereas *O. occidentalis* is a solitary phytophage that oviposits after the capitula begin to open and whose larvae feed on the floral tubes and maturing achenes. Thus *O. occidentalis* employs Zwölfer's second trophic strategy. *Rotruda mucidella* and *P. carduidactyla* follow Zwölfer's third trophic strategy as highly mobile, indiscriminate feeders (Goeden and Ricker 1986b, 1987a, b).

Resource sharing.—Resource sharing by *P. gentilis* larvae in capitula of *C. californicum* involved avoidance of intraspecific competition for food early in their life cycle. Females oviposit eggs singly or in clusters

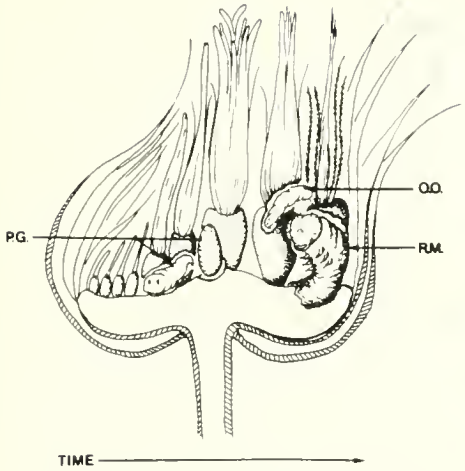

Fig. 2. Temporal and spatial partitioning (diagrammatic) of a thistle capitulum by three of the most common insect species comprising a complete guild in southern California. P.G., *P. gentilis*; O.O., *O. occidentalis*; R.M., *R. mucidella*.

of up to 13 centrally in the capitula (Headrick and Goeden 1990 and unpublished data). After eclosion, first instars tunnel into separate, nearby floral tubes where they feed for the entire stadium. Second instars leave these initially attacked floral tubes and tunnel towards the outer margin of the capitula through a series of floral tubes well above the level of the achenes. Thus, central placement of the eggs and differences in feeding modes between the first two instars minimized competition between these instars in capitula of *C. californicum*. Third instar feeding was confined to the central ovules, and as noted below, scored the upper receptacle at higher larval densities despite the presence of an outer ring of uneaten ovules remaining in the capitulum.

Interspecific competition in *C. proteanum* was avoided among guild members by temporal and spatial division of the capitula resources (Fig. 2). *Paracantha gentilis* avoided substantial interspecific competition because it attacked early and fed and pupariated centrally at anthesis surrounded by a mixture of dried feces and fragments of floral tubes and pappus hairs. This type

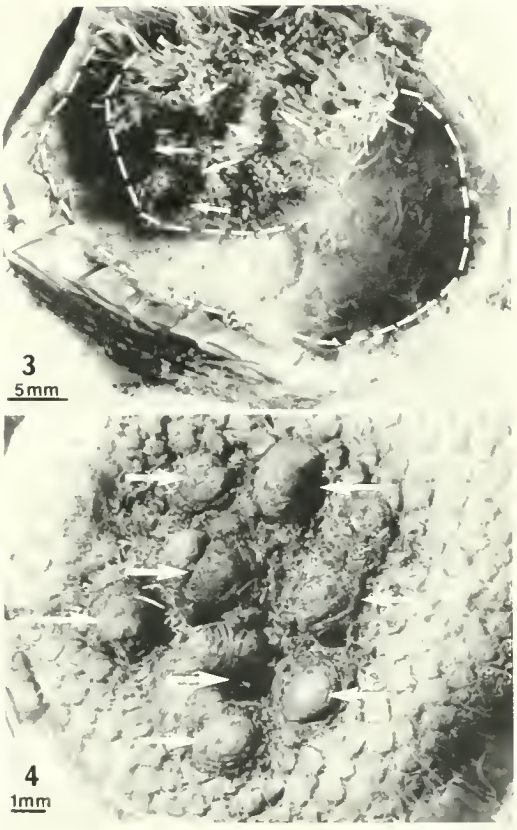

Fig. 3. Face view of dissected *C. proteanum* capitulum showing peripheral feeding path of *R. mucidella* (dotted-line), arrows show tops of centrally located *P. gentilis* puparia.

Fig. 4. Face view of receptacle of *C. californicum* pitted with *P. gentilis* cups formed by third instars.

Fig. 5. Cross-section of receptacle of *C. californicum* with *P. gentilis* puparium cupped in feeding cavity, dotted line denotes receptacle surface.

Table 2. *Cirsium californicum* capitula dissected (n = 107) containing late 3rd instar larvae or puparia, and the percentage of infested capitula with receptacle scoring by larvae.

	Infestation Class: No. 3rd Instar Larvae or Puparia per Capitulum						
	1	2	3	4	5	6	7
No. of capitula per class	32	27	23	8	4	3	2
No. (%) of capitula per class with receptacle scored	2 (6)	4 (15)	15 (65)	5 (62)	3 (75)	3 (100)	2 (100)

of spatial evasion was first recognized by Zwölfer (1979) for thistle-feeding tephritids in Europe, where he suggested it mitigated the effects of interspecific competition.

In contrast to *P. gentilis, O. occidentalis* and *R. mucidella* typically feed on the peripheral achenes (Figs. 2, 3). The value of this avoidance behavior was illustrated by dissection of a capitulum in which a *P. gentilis* larva had pupariated angled ca. 45° from a normal position perpendicular to the receptacle. The adult emerged abnormally towards the side of the capitulum, crossing the path of a *R. mucidella* larva which ate through it, leaving the head and abdomen behind!

Third instar feeding.—Dissection of infested *C. californicum* capitula also led to the discovery that if three or more *P. gentilis* third instar larvae were present in a capitulum, at least one had scored the upper receptacle centrally. In all capitula dissected, this receptacle feeding formed uniform cup-like depressions, 1.6 ± 0.09 ($\bar{x}$ ± S.E.) mm wide and 1–2 mm deep (n = 35) (Figs. 4, 5). The uniform depth and width of these depressions suggested a specialized function as sources of sap upon which the older larvae fed at higher larval densities. The mouthparts of the third instar, including the newly discovered "median oral lobe," show modification for such liquid food uptake (Headrick and Goeden 1990). Fluid feeding by larvae of Tephritidae in galls, capitula, and other plant parts may be underappreciated in its importance and occurrence.

Romstöck (1987) reported that larvae of *Tephritis conura* Loew induced a callus while feeding in the receptacle of *Cirsium heterophyllum* (L.) Hill. This structure then acted as a "sink" to maintain the nutrient flow to the head, much like a gall (Zwölfer 1985). That tephritid galls act as metabolic sinks in capitula of knapweeds (Subtribe Centaurinae), close relatives of *Cirsium* thistles (Subtribe Carduinae) was well demonstrated experimentally by Harris (1980). Thus, *T. conura* larvae similarly were found to induce and use callus formation to extend their resource limits, because the immature capitulum *per se* was a finite resource that did not contain enough nutrients to support completion of larval development. With *P. gentilis*, there was no induction of callus tissue or a gall, probably because receptacle scoring occurs after the meristematic stage and tissue differentiation (Harris 1980, 1989). Larval feeding apparently involves the slow, continual erosion and re-wounding of the upper receptacle during feeding-cavity formation to insure continued sap flow. In this manner, immature closed capitula of limited biomass can sustain several *P. gentilis* larvae.

This feeding mode is distinct from the receptacle feeding exhibited by species of *Cirsium*-head-infesting tephritids in Europe (Zwölfer 1988, Harris 1989) and elsewhere in North America (Steck 1984). As described by Steck (1984), *Chaetostomella undosa* (Coquillett) larvae bored into and fed on the receptacle tissues during all three instars. When larval densities were high, and after the receptacle was consumed, they mined downwards into the peduncle and stem. The scheme of Harris (1989) limits

Table 2. Extended.

Infestation Class: No. 3rd Instar Larvae or Puparia per Capitulum				
8	9	10	11	12
1	3	1	0	2
1 (100)	3 (100)	1 (100)	—	2 (100)

receptacle feeding by non-gall formers to immature "buds," but *C. undosa* continues to mine the receptacle through floret and achene growth stages (Steck 1984). *Paracantha gentilis* co-existed with *C. undosa* and was the dominant phytophage in *Cirsium* capitula sampled by Steck (1984). No other species of non-gall-forming, ovule or soft achene-feeding Tephritidae has yet been reported to feed on the ovules and then score the receptacle in the manner of *P. gentilis*, cf. Tauber and Toschi (1965), Stegmaier (1967), Cavender and Goeden (1982, 1984), Lamp and McCarty (1982), Goeden (1987), and Goeden et al. (1987). These data also clearly demonstrate that tephritids associated with Nearctic *Cirsium* spp. show novel feeding habits distinct from Palearctic tephritids (Zwölfer 1988, Harris 1989).

This change in third instar feeding patterns was analyzed in capitula containing only *P. gentilis* larvae. The average number of third instars found in 107 infested capitula was 3.3 ± 0.3 (range, 1–12). The receptacle diameter (used as an index of available resources) was highly correlated with the number of achenes per capitulum (corr. coeff. = 0.851, $P = 0.001$, n = 25). However, there was no significant correlation between the diameter of the receptacle and the number of larvae in a given capitulum, so the size of a capitulum did not limit infestation density.

Dissections showed, instead, that the age of the third instar as well as larval density determined the feeding mode. When capitula contained fewer than three third instar larvae, they usually fed centrally on the ovules and pupariated without scoring the receptacle (Table 2). A change in third instar feeding behavior took place in capitula with three or more individuals; instead of continuing to feed on the ovules, at least one, possibly the smallest and/or the youngest, third instar(s) scored the receptacle. This occurred in 65% of all the capitula dissected containing three third instars. All capitula containing six or more (up to 12) third instar larvae had scored receptacles (Table 2).

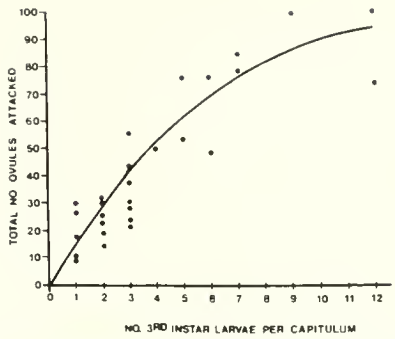

Fig. 6. Relationship of total ovules attacked per capitulum and *P. gentilis* third instar density.

Zwölfer (1985) noted that the number of achenes (ovules) attacked was a more precise measurement of resource utilization than the percentage of capitula attacked. However, in capitula of *C. californicum* containing from three to 12 puparia, complete consumption of the ovules never was detected. The number of ovules attacked per larva decreased as densities rose (Fig. 6). This decrease was not due to a depletion of resources (ovules), intraspecific competition and larval starvation, as suggested for *P. culta* (Wiedemann) by Lamp and McCarty (1982). Instead, this reflected a new resource, i.e. the receptacle, being used along with the central ovules by the younger third instars. Therefore, the precision of the statistic for resource utilization is dependent on the feeding strategy of the species of Tephritidae involved.

Ecological significance.—By not consuming all the achenes in a capitulum, *P. gentilis* followed the strategy of "evasion," as de-

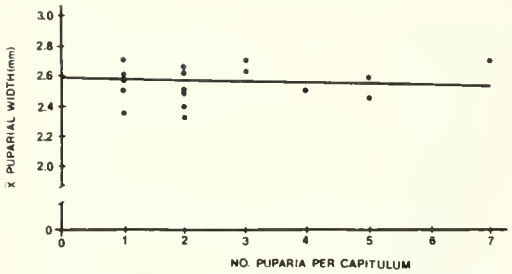

Fig. 7. Relationship of mean pupal width of *P. gentilis* per capitulum of *C. californicum* to pupal density (corr. coeff. = 0.059, n.s.).

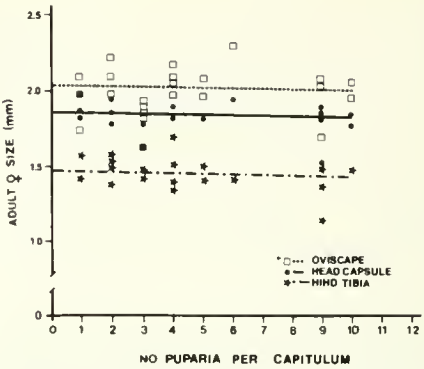

Fig. 8. Relationship of three *P. gentilis* adult female measurements (max. head width, hind tibia length, oviscape length) to pupal *P. gentilis* density per capitulum (corr. coeff. = 0.181, 0.154, 0.033, respectively, n.s., n = 27).

fined by Zwölfer (1979) for thistle-head-infesting tephritids. However, the strategy of a "non-interactive grazing system" in which the phytophages merely consume a surplus of seeds produced (Zwölfer 1979) does not apply to *P. gentilis* in *C. proteanum* capitula. At the Sawmill Mt. location, where the guild was complete, i.e. at least three insect species infested the capitula, total consumption of achenes occurred in 60% of 50 infested capitula dissected. *Paracantha gentilis* had the advantage in this system by its optional use of an evasion strategy, i.e. being able to augment ovule-feeding with another, replenishable resource—plant sap from the receptacle. In this manner, *P. gentilis* avoided most competition from other guild members as well as among its siblings at high densities.

Several parameters were measured on adults reared from puparia dissected from capitula containing one to 12 individuals to determine if there were any effects of upper receptacle-moderated sap-feeding on puparial and adult sizes. No significant difference in puparial widths was found among individuals in capitula containing low and high fly densities (Fig. 7). Percentage adult emergence showed no differences among capitula containing different numbers of puparia, i.e. 54 of 58 (91.8%) adults emerged from unparasitized puparia. Head widths, hind tibial lengths and oviscape lengths of adult females also showed no significant correlation among flies that emerged from capitula containing low or high numbers of puparia (Fig. 8).

Conclusion

The trophic strategy involving early-aggregated attack in capitula by Tephritidae, as now studied with both Palearctic and Nearctic species, shows three types of adaptations to extend and partition a finite resource, the capitulum. These adaptations involve tephritids that induce galls in the immature capitula (Zwölfer 1985); callus-forming tephritids (Romstöck 1987); and as reported in the present study, a receptacle-scoring tephritid that induces no plant tissue growth, and thus directly feeds on assimilates channelled to the immature capitulum.

Is *Paracantha gentilis* evolving towards gall formation? According to Zwölfer (1983), the most evolutionarily advanced insect-thistle capitulum relationship is gall formation. This implies an intimate, long evolved relationship between insect and host plant. However, Zwölfer (1988) noted that tephritid species maintained their trophic preadaptations during host transfer, i.e. gall-formers induced galls on any new host. By this interpretation, *P. gentilis* was preadapted to feed in *Cirsium* capitula without inducing tissue proliferation. But, is the change

to receptacle feeding by third instars also a pre-adapted feeding response to infestation densities, or an evolved adaptation to reduce inter- and intraspecific competition within thistle capitula? If it is the latter, *P. gentilis* may further evolve into a gall former. North American *Cirsium* thistles lack gall-forming insect associations (Goeden and Ricker 1987b). Supplementing findings by Zwölfer (1985, 1988) and Romstöck (1987), we suggest that receptacle scoring by *P. gentilis* represents just one end of a spectrum of feeding strategies evolved by thistle-head infesting tephritids, i.e. a new category of an early aggregated attacker that makes use of an immature capitulum in a unique manner to support its larval development without recourse to gall or callus tissue formation. In this manner the infested, closed, immature capitulum itself acts like a gall, offering the larvae a food source and constant micro-environment protected from desiccation, predation, and most parasitoids (Headrick and Goeden 1989b).

The "feeding niche" of *P. gentilis* in thistle capitula is thus novel by European criteria (Zwölfer 1988, Harris 1989). Therefore, it and associated herbivores exemplify the failure of phytophage communities to converge in structure despite similar resources on different continents, as demonstrated with bracken (*Pteridium aquilinium* (L.) Khn.) and its herbivores in England, New Mexico, and South Africa by Lawton (1976, 1982) and Compton et al. (1989).

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TARSAL AND OVIPOSITOR SENSILLA OF *HELIOTHIS VIRESCENS* AND *H. SUBFLEXA* (LEPIDOPTERA: NOCTUIDAE)

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Abstract.—Three types of sensilla are present on the tarsi of *Heliothis virescens* and *H. subflexa*; a long, fluted sensillum chaeticum and short and long sensilla trichodea. The number of these sensilla varies from tarsus to tarsus within a species and between species. Females of *H. virescens* have significantly more of each type than females of *H. subflexa* and the males of *H. virescens*. Tarsus II bears the most of each type of sensillum; tarsus III has the fewest. The ovipositor of each species does not differ in the types and number of sensilla. Long and short sensilla chaetica can be found on most areas of the ovipositor whereas the 5 or 6 sensilla trichodea are situated on the apex of each valve. The surface of each valve is covered by short, pointed microtrichia.

Key Words: Noctuidae, *Heliothis*, tarsus, ovipositor, sensilla

Olfactory receptors, contact chemoreceptors, mechanoreceptors and visual receptors that are situated on various insect body regions such as the antennae, legs and ovipositor are involved in host finding (Dethier 1982, Miller and Strickler 1984, Ramaswamy 1988). Little is known about the role of tarsi and ovipositor in selection of an oviposition site by adult Lepidoptera. Most of the early morphological and behavioral research on adult Lepidoptera dealing with host plant selection is on butterflies (Minnich 1921, 1922a, b, Fox 1966, Ma and Schoonhoven 1973, Calvert 1974, Calvert and Hanson 1983, Renou 1983).

Many species in the family Noctuidae are serious pests on a wide variety of important agricultural crops throughout the world but our knowledge is scarce about what role sensory receptors on the tarsi and ovipositor play in host-plant finding. Tarsal and ovipositor sensory receptors are known to have an important role in host plant selection in moths such as *Chilo partellus* (Swinhoe) and *Spodoptera littoralis* (Boisd.), by responding to various chemical and mechanical stimuli (Chadha and Roome 1980, Waladde 1983, Salama et al. 1984, Waladde et al. 1985). There are several important pest species in the genus *Heliothis*, at present only one paper (Ramaswamy et al. 1987) deals with the possible role of sensory receptors on the tarsi and ovipositor in host plant selection for oviposition of *H. virescens* (F.). The purpose of the present study is to provide information on the morphology, number and distribution of sensory receptors on the tarsi and ovipositor of *H. virescens*, which has a wide host plant range, and to compare this species to *H. subflexa*, which has a very restricted host plant range.

MATERIALS AND METHODS

Specimens for scanning electron microscopy were fixed in 4% glutaraldehyde in Na-cacodylate buffer (pH 7.1) for 8 h at 4°C. They were washed in the same buffer and post-fixed in 2% osmium tetroxide for 24

Figs. 1–3. Tarsi of *H. virescens* female. 1, Tarsus I. 2, Tarsus II. 3, Tarsus III.

Table 1. Comparison of the number of sensilla on the tarsi of *H. virescens* females.

Tarsus	A	B	C
I	21.88 ± 0.83 b	42.75 ± 1.04 b	11.46 ± 0.52 b
II	23.63 ± 0.74 a	45.25 ± 0.89 a	12.81 ± 0.71 a
III	14.88 ± 0.64 c	32.50 ± 0.93 c	9.43 ± 0.67 c

A = sensillum chaeticum; B = short sensillum trichodeum; C = long sensillum trichodeum. Means within a column not followed by the same letter are significantly different ($P < 0.05$) as determined by ANOVA followed by Student-Newman-Keuls Test (n = 8).

h. After dehydration in a graded series of ethanol, the specimens were placed in pentane overnight and then air dried. The tarsi and ovipositors were sputter-coated with gold-palladium and examined with a JEOL JSM-35 CF scanning electron microscope at 20 kV.

The legs of eight female *H. virescens* and *H. subflexa* and eight male *H. virescens* were cleared in 7% KOH and mounted in euparal. The data on the number of sensory receptors on tarsi I–III are given as a mean plus the standard deviation and were subjected to ANOVA followed by Student-Newman-Keuls Test ($P < 0.05$). A *t*-test ($P < 0.05$) was used for the comparison of the number of sensory receptors on each tarsus of *H. virescens* and *H. subflexa* females and *H. virescens* female and male.

Results and Discussion

Tarsi.—The tarsi consist of 5 tarsomeres and a pretarsus. Scales cover the dorsal surface of each tarsus whereas on the ventral surface of each tarsus there is an area that is devoid of scales (Figs. 1–3). This area is the contact region between the tarsus and substrate. The total area that comes in contact with the substrate differs for tarsi I–III (Figs. 1–3). It is from this region that the number of various types of sensory receptors was counted. Tarsus II has the largest contact area and the greatest number of sensory receptors, followed by tarsi I and III (Figs. 1–3; Tables 1, 2).

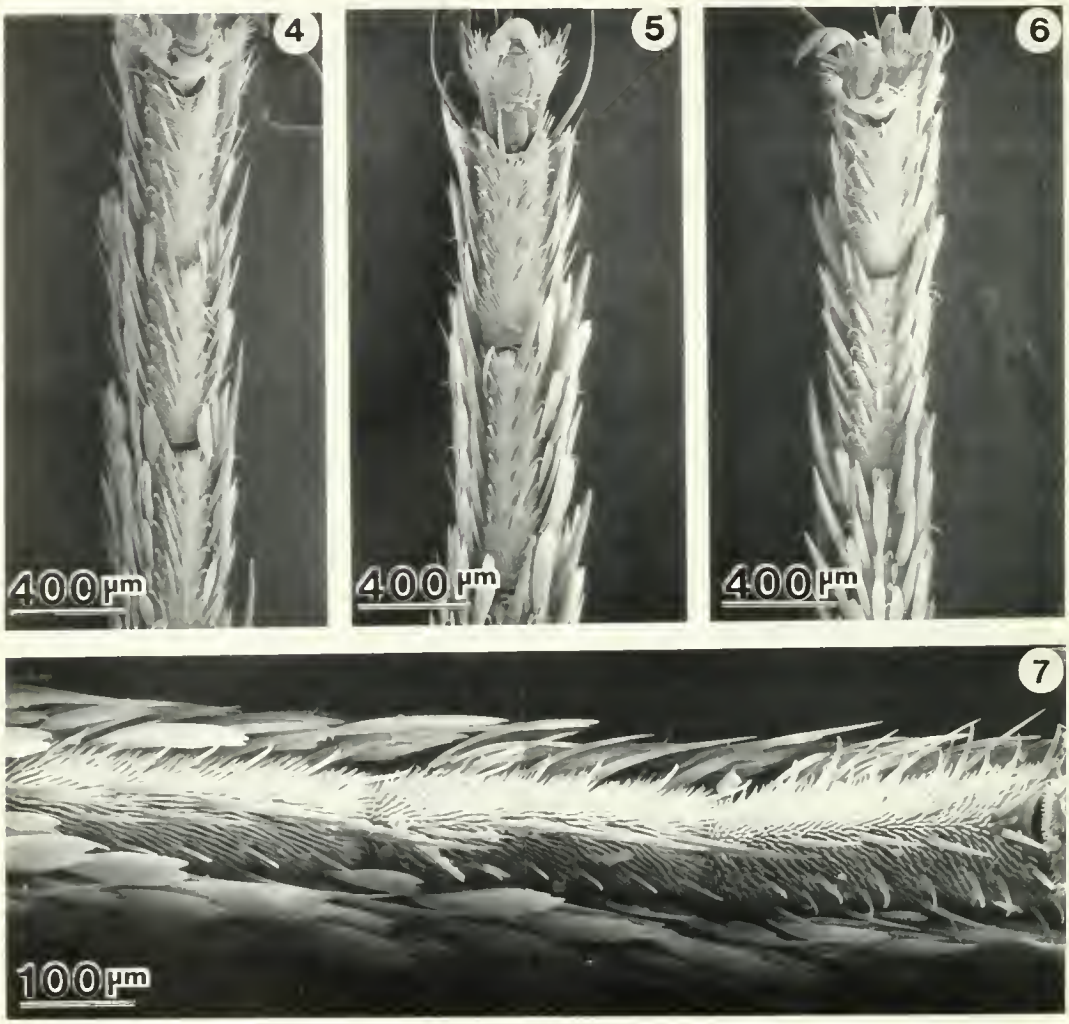
The long trichoid sensilla are also located on the periphery of the contact region and at the apex of tarsomere V (Fig. 1). Two long trichoid sensilla are apically located on tarsomere V on either side of the tarsomere midline (Fig. 1). This sensory receptor is 65–85 μm long and curves back in the direction of the body (Figs. 1, 8). A distinct cuticular pattern covers the surface of the sensillum from the base to the apex (Fig. 9).

On each tarsus there are 3 rows of sensilla chaetica, 1 row on each side of the contact region and the third row set off-centre on tarsus I and on the midline of tarsi II and III (Figs. 1–3). This pattern is the same for the female and male of *H. virescens* and *H. subflexa* female (Figs. 1–7). The sensillum

Table 2. Comparison of the number of sensilla on the tarsi of *H. subflexa* females.

Tarsus	A	B	C
I	18.13 ± 0.99 a	37.88 ± 0.83 a	9.31 ± 0.64 a
II	12.13 ± 0.98 b	28.00 ± 0.76 b	6.78 ± 0.81 b
III	11.75 ± 0.71 b	27.88 ± 0.64 b	6.12 ± 0.77 b

A = sensillum chaeticum; B = short sensillum trichodeum; C = long sensillum trichodeum. Means within a column not followed by the same letter are significantly different ($P < 0.05$) as determined by ANOVA followed by Student-Newman-Keuls Test (n = 8).

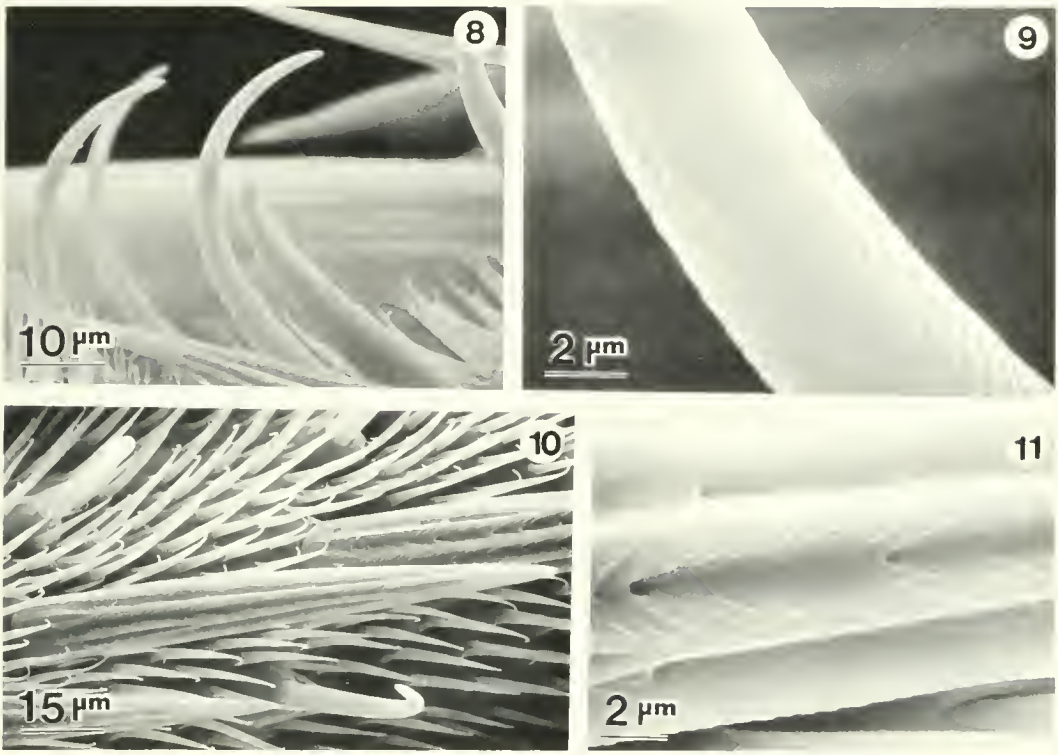


Figs. 4–7. 4–6, Tarsi of *H. subflexa* female. 4, Tarsus I. 5, Tarsus II. 6, Tarsus III. 7, Tarsus I of *H. virescens* male.

chaeticum has a socket at the base, tapers and slants downward in the direction of the pre-tarsus (Fig. 1). The surface of this sensory receptor has large, longitudinal ridges possessing secondary ridges on its surface and pits are situated at the base of the large ridges (Figs. 10, 11). This type of sensillum ranges from 80–165 µm long.

Two rows of short trichoid sensilla that are situated on either side of the central row of sensilla chaetica are on each tarsus in the contact region (Fig. 1). There are 2 distinct types of short trichoid sensilla. The first type if 42–46 µm long and 7–9 µm wide at the base and is slightly curved near the apex (Fig. 12). The receptor surface is covered with irregular longitudinal striations (Fig. 13). The second type of short trichoid sensillum is 39–43 µm long and 5–6.5 µm wide at the base, with the apical third distinctly hooked (Fig. 12). The receptor surface has irregular, lateral striations (Fig. 14).

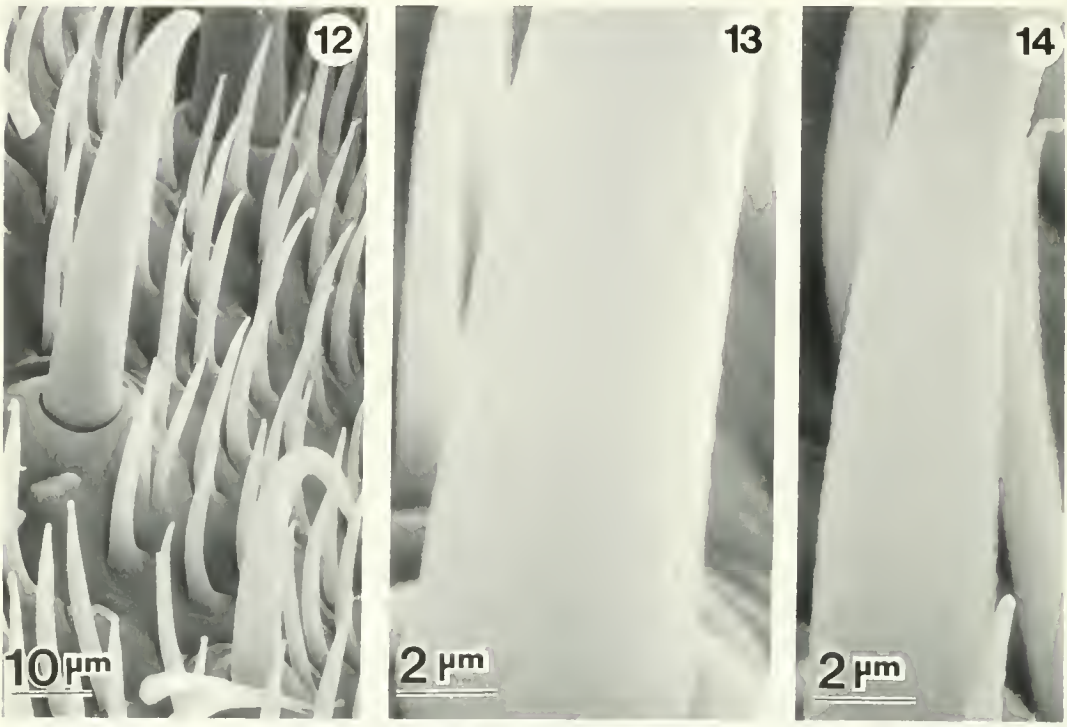
The distribution pattern and morphological types of sensilla that are found on the



Figs. 8–11. 8, Long sensilla trichodea. 9, Surface pattern on the long sensillum trichodeum. 10, Sensillum chaeticum. 11, Surface pattern on the sensillum chaeticum.

tarsi of female *H. virescens* and *H. subflexa,* and male *H. virescens* are similar in that each tarsus has 2 outer rows of sensilla chaetica and long trichoid sensilla, a central row of sensilla chaetica and a row of short trichoid sensilla on either side of the central row of sensilla chaetica (Figs. 1–7). The number of sensory receptors differs on each tarsus. In females of *H. virescens* and *H. subflexa* the number of sensilla chaetica and long and short trichoid sensilla show the same pattern in that tarsus II > tarsus I > tarsus III (Tables 1, 2). There is a significant difference between *H. virescens* and *H. subflexa* females in the number of sensory receptors on each tarsus in that *H. virescens* has the greater number of each sensillar type (Table 3). The pattern in the number of sensory receptors on the male tarsi of *H. virescens* differs from the female in that tarsus I has significantly more long and short trichoid sensilla and sensilla chaetica than tarsi II and III which have similar numbers of sensillar types (Table 4). Females of *H. virescens* have significantly more of all sensillar types than the males (Table 5).

Similar sensilla chaetica and trichodea on the tarsi of *H. virescens* and *H. subflexa* are also located on the tarsi of other moth species such as *Chilo partellus* and *Eldana saccharina* (Waladde 1983), and *Helicoverpa zea* (Callahan 1969), but there are no data on the distribution and number of each sensillar type on the tarsus of each leg. These types of sensilla are present on the tarsi of females and males of *Pieris brassicae* and the distribution pattern is similar to what is found on *H. virescens* and *H. subflexa.* The number of sensilla chaetica on the tarsi of *Chlosyne lacina* Geyer and *Heliconius*



Figs. 12–14. Short sensilla trichodea. 12, Straight and hooked forms. 13, Surface of the straight form. 14, Surface of the hooked form.

charitonius L. is greatly reduced, and this type of sensillum is often associated with a cluster of trichoid sensilla (Calvert 1974, Renou 1983).

Electrophysiological experiments on several species of Lepidoptera showed that the trichoid sensilla respond to salt, sugar and plant substances (Morita et al. 1957, Takeda 1961, Ma and Schoonhoven 1973, Renou 1983, Waladde 1983, Waladde et al. 1985). Behavioral tests involving the tarsi indicate the importance of tarsal sensory receptors for host plant acceptance and oviposition (Ma and Schoonhoven 1973, Calvert and Hanson 1983, Salama et al. 1984, Faucheux 1985).

The trichoid sensilla on the tarsi of *H. virescens* respond to salts, sugars and plant extracts (Ramaswamy and Hanson unpublished data), and behavioral experiments

Table 3. Comparison of the number of sensilla on the tarsi of *H. virescens* males.

Tarsus	A	B	C
I	18.38 ± 0.92 b	38.50 ± 0.93 b	9.71 ± 0.59 b
II	22.00 ± 0.76 a	42.88 ± 0.99 a	11.34 ± 0.68 a
III	12.63 ± 0.91 c	26.75 ± 1.49 c	8.18 ± 0.52 c

A = sensillum chaeticum; B = short sensillum trichodeum; C = long sensillum trichodeum. Means within a column not followed by the same letter are significantly different ($P < 0.05$) as determined by ANOVA followed by Student-Newman-Keuls Test (n = 8).

Table 4. Comparison of the number of sensilla on the tarsi of *H. virescens* and *H. subflexa* females.

Tarsus	A	B	C
H. v. I	21.88 ± 0.83 a	42.75 ± 1.04 a	11.46 ± 0.52 a
H. s. I	18.38 ± 0.92 b	38.50 ± 0.93 b	9.71 ± 0.59 b
H. v. II	23.63 ± 0.74 a	45.25 ± 0.89 a	12.81 ± 0.71 a
H. s. II	22.00 ± 0.76 b	42.88 ± 0.99 b	11.34 ± 0.58 b
H. v. III	14.88 ± 0.64 a	32.50 ± 0.93 a	9.43 ± 0.67 a
H. s. III	12.63 ± 0.92 b	26.75 ± 0.49 b	8.18 ± 0.52 b

A = sensillum chaeticum; B = short sensillum trichodeum; C = long sensillum trichodeum. Means not followed by the same letter are significantly different ($P < 0.05$) as determined by Student's-*t*-test (n = 8).

showed that the sensory receptors on the tarsi are involved in host plant acceptance and oviposition (Ramaswamy et al. 1987). *Heliothis virescens* oviposits on a wide variety of host plants, such as tobacco, cotton, peanut and tomato, whereas *H. subflexa* uses ground cherry. This difference is the number of host plants for oviposition may be due in part to the difference in the number of sensory receptors found on the tarsi of both species.

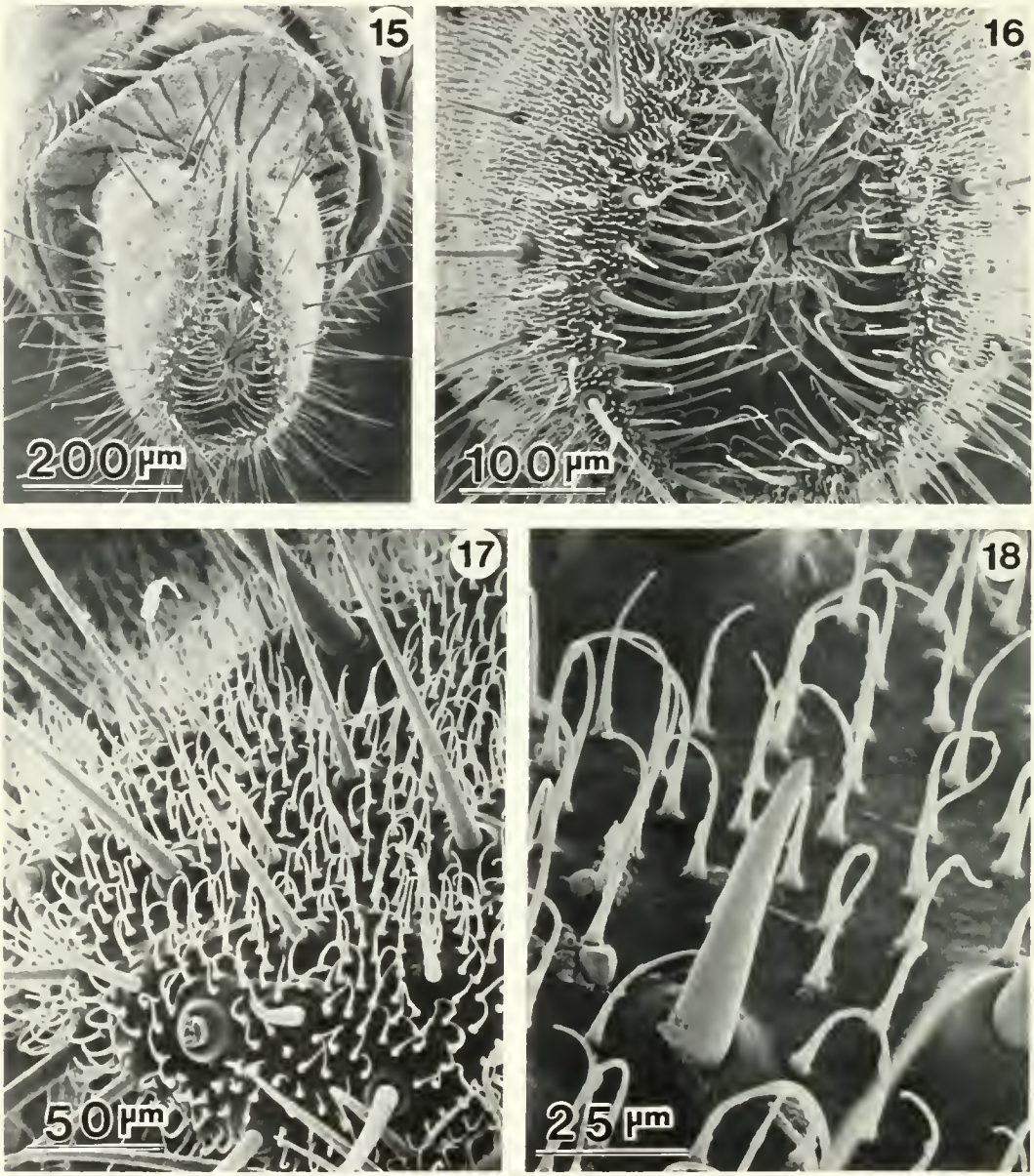
Ovipositor.—The ovipositor consists of two papillae anales that are on either side of the oviduct and anal openings (Fig. 15). The oviduct opening is surrounded by short and long sensilla chaetica which have tapered tips and smooth walls (Fig. 16). These sensilla are also situated on the rest of the ovipositor surface (Fig. 17). The apex of the ovipositor bears blunt-tipped trichoid sensilla which have shallow longitudinal grooves on the surface that-fade near the apex of the sensillum (Fig. 18). Each papillae anales has five to six of these trichoid sensilla. The remainder of the ovipositor surface is covered with microtrichia.

There are no differences in the morphology, number and distribution of the sensilla between *H. virescens* and *H. subflexa*. The trichoid sensilla on the ovipositor of *Phthorimaea operculella* (Zell.) (Gelechiidae) are contact chemoreceptors that are involved in oviposition on a suitable substrate (Fenmore 1978, Valencia and Rice 1982). Additionally these sensilla are present on the ovipositor of noctuid species such as *Chilo partellus* and *Spodoptera littoralis*, and morphological and electrophysiological data indicate that they are contact chemoreceptors (Chadha and Roome 1980, Waladde 1983, Waladde et al. 1985). But the exact role(s) these contact chemoreceptors

Table 5. Comparison of the number of sensilla on the tarsi of *H. virescens* females and males.

Tarsus	A	B	C
H. v. f I	21.88 ± 0.83 a	42.75 ± 1.04 a	11.46 ± 0.52 a
H. v. m I	18.13 ± 0.99 b	37.88 ± 0.83 b	9.31 ± 0.64 b
H. v. f II	23.63 ± 0.74 a	45.25 ± 0.89 a	12.81 ± 0.71 a
H. v. m II	12.13 ± 0.98 b	28.00 ± 0.64 b	6.78 ± 0.81 b
H. v. f III	14.88 ± 0.64 a	32.50 ± 0.95 a	9.43 ± 0.67 a
H. v. m III	11.75 ± 0.71 b	27.88 ± 0.64 b	6.12 ± 0.77 b

A = sensillum chaeticum; B = short sensillum trichodeum; C = long sensillum trichodeum. Means not followed by the same letter are significantly different ($P < 0.05$) as determined by Student-*t*-test (n = 8).



Figs. 15–18. Ovipositor of *H. virescens*. 15, Two papillae anales surrounding the anal and oviduct openings. 16, Short and long sensilla chaetica around the oviduct opening. 17, Sensillum trichodeum amongst the long and short sensilla chaetica. 18, Sensillum trichodeum with a slightly grooved surface.

play in oviposition behavior of the above mentioned species and *H. virescens* and *H. subflexa* needs to be determined.

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A NEW GENUS *NANCYANA* AND NINE NEW SPECIES WITH A REVIEW OF THE RELATED GENUS *RHOGOSANA* (HOMOPTERA: CICADELLIDAE)

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Abstract.—The new genus ***Nancyana*** and nine new species, ***N. agitata***, ***N. gadouae***, ***N. lubrica***, ***N. fernandezi***, ***N. fasciata*** from Venezuela; ***N. bordoni*** from Argentina; ***N. curva***, ***N. isoclada***, ***N. abluta*** from the Guyanas are described. Two species transferred from *Rhogosana* are also included in this genus, *N. aldeia* (DeLong) (type species) **new combination**, and *N. duida* (DeLong) **new combination**. The other species added to *Rhogosana* by DeLong are transferred as follows: *Folicana amazona* (DeLong) **new combination** (= *marra* Freytag) **new synonym**, and *F. fosteri* (DeLong) **new combination** (= *robusta* Osborn) **new synonym**, and *Gypona* (*Marganalana*) *brazilia* (DeLong) **new combination**.

Key Words: Cicadellidae, Gyponinae, leafhoppers, *Nancyana, Rhogosana, Folicana, Gypona*

On reviewing the species of *Rhogosana* Osborn it was found that all of the species added to this genus (DeLong 1975, 1981) belong to different genera. In this paper a new genus is set up for two of the species and nine new species. This genus is closely related to *Rhogosana* but can be separated from it on external color pattern and male genitalic characters.

The remaining three species are transferred to other genera as follows:

brazilia DeLong 1975 (transferred to *Gypona* Germar in the subgenus *Marganalana* Metcalf, New Combination.

amazona DeLong 1981 transferred to *Folicana* DeLong and Freytag (= *marra* Freytag 1979), New Combination and New Synonym.

fosteri DeLong 1981 transferred to *Folicana* (= *robusta* Osborn 1938), New Combination and New Synonym.

This leaves *Rhogosana* monotypic with just the type species *rugulosa* (Osborn). This species appears quite primitive being very large and unicolorous, and unique in that the male genitalia are quite different from other genera in this subfamily.

Genus *Nancyana*, NEW GENUS

Crown short, broadly rounded, three times as wide between eyes at base as median length, with a definite foliaceous margin, disc smooth usually without striae. Head narrower than pronotum. Ocelli prominent, slightly closer to median line than to eyes, slightly nearer posterior than anterior margin of head. Aedeagus with basal processes (paraphyses) and two pair of subapical processes. Pygofer bifurcate at apex. Usually unicolorous, greenish brown or brown on head and pronotum; forewings darker brown with many spots of brown or black, sometimes spots on forewings forming a pattern.

Type species: Rhogosana aldeia DeLong.

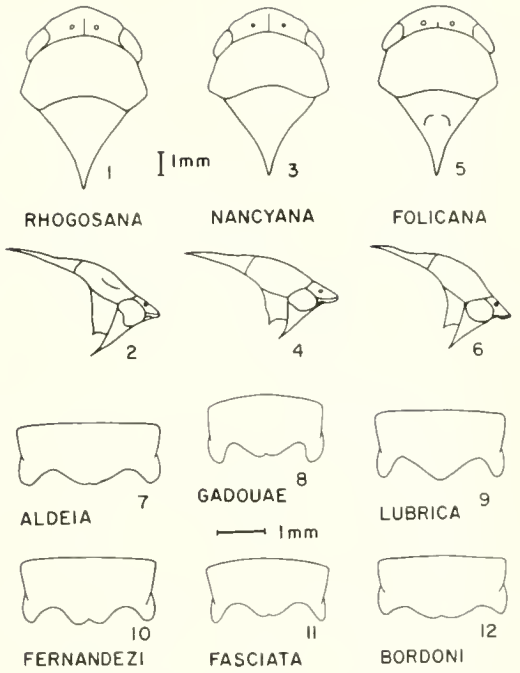
This genus is closely related to *Rhogosana* and *Folicana*, but the color pattern and the male genitalia of the species included in this genus are quite different and warrant the

separation of this genus. A comparison of some of the morphological characters of these three genera are given in Figs. 1–6. Most species of this genus can easily be recognized by being over 12 mm in length, with the head foliaceous, with the head, pronotum and scutellum smooth and evenly colored; and with the forewings darker colored and usually speckled or spotted. This genus is named for my first wife who died in 1984.

Key to the Genus *Nancyana*

(Males of *gadouae, lubrica, fernandezi, fasciata, bordoni* and *curva*; and females of *abluta, agitata, isoclada* and *duida* are not known.)

1. Males 2
1′. Females 6
2. Aedeagus with both pairs of subapical processes sharply pointed (Fig. 34) ..... *duida* (DeLong)
2′. Aedeagus with one pair of subapical processes sharply pointed, other pair truncate at apex (Fig. 24) 3
3. Aedeagus with both pairs of subapical processes equal in length and lying in same plane in lateral view (Fig. 19) ..... *isoclada* sp. n.
3′. Aedeagus with both pairs of subapical processes not equal in length or not lying in same plane in lateral view (Figs. 14, 29) 4
4. Aedeagus with outer pointed subapical processes wider at base and extending ventrally (Figs. 13, 14) ..... *agitata* sp. n.
4′. Aedeagus with outer pointed subapical processes not greatly wider at base and extending dorsally (Figs. 28, 29) 5
5. Aedeagus with outer pointed subapical processes shorter than inner truncate subapical processes (Fig. 29) ..... *aldeia* (DeLong)
5′. Aedeagus with outer pointed subapical processes nearly same length as inner truncate subapical processes (Fig. 24) ..... *abluta* sp. n.
6. Forewing with a distinct pattern as in Fig. 43 ..... *curva* sp. n.
6′. Forewing with an indistinct pattern (Figs. 38–42) 7
7. Forewing shiny, polished; seventh sternum as in Fig. 12 ..... *bordoni* sp. n.
7′. Forewing not shiny or polished; seventh sternum with posterior margin usually more deeply emarginate (Figs. 10, 11) 8
8. Seventh sternum with median triangular (Fig. 9) ..... *lubrica* sp. n.
8′. Seventh sternum with median rounded and emarginate (Fig. 11) 9
9. Seventh sternum with median obviously emarginate (Fig. 10) ..... *fernandezi* sp. n.
9′. Seventh sternum only lightly emarginate (Fig. 11) 10
10. Seventh sternum with median same length as lateral margins (Fig. 7) ..... *aldeia* (DeLong)
10′. Seventh sternum with median shorter than lateral margins (Fig. 8) 11
11. Seventh sternum with lateral margins rounded ..... *gadouae* sp. n.
11′. Seventh sternum with lateral margins pointed ..... *fasciata* sp. n.



Figs. 1, 2. *Rhogosana rugulosa* (Osborn). 1. Dorsal view of head, pronotum and scutellum. 2. Lateral view of head, pronotum and scutellum. Figs. 1–6 drawn to same scale.

Figs. 3, 4. *Nancyana aldeia* (DeLong). 3. Dorsal view of head, pronotum and scutellum. 4. Lateral view of head, pronotum and scutellum.

Figs. 5, 6. *Folicana zella* Freytag. 5. Dorsal view of head, pronotum and scutellum. 6. Lateral view of head, pronotum and scutellum.

Figs. 7–12. Female seventh sternum, ventral view. 7. *Nancyana aldeia* (DeLong). 8. *N. gadouae* sp. n. 9. *N. lubrica* sp. n. 10. *N. fernandezi* sp. n. 11. *N. fasciata* sp. n. 12. *N. bordoni* sp. n. All drawn to the same scale.

Nancyana duida (DeLong)
NEW COMBINATION
(Figs. 33–37)

Rhogosana duida DeLong, 1975 (type locality—Mt. Duida, Venezuela).

Length of male 15 mm, female unknown. Crown broadly rounded, three times as wide at base between eyes as median length.

Color: Head, pronotum and scutellum uniformly dull yellow brown. Forewings brown mottled with creamy brown spots.

Male genitalia: Pygofer rounded, with triangular lobe at apical margin. Genital plate long, nearly four times as long as wide, truncate at apex. Style with apex blunt, nearly truncate but slightly protruding on dorsal and ventral margins. Aedeagus with broad shaft, two pairs of subapical processes, half length of shaft, sharply pointed at apex; base robust, with a pair of basal processes from base to ventral side of shaft extending to pointed apices two thirds length of shaft.

Type: Holotype male, in the American Museum of Natural History.

Note: The holotype was examined and used for the illustrations. No other specimens of this species have been seen. The paratype male from Brazil was not examined and can not be verified as belonging to this species. This species is similar to *aldeia*, except slightly larger and with distinct male genitalia.

Nancyana aldeia (DeLong)
NEW COMBINATION
(Figs. 7, 28–32, 38)

Rhogosana aldeia DeLong, 1975 (type locality—Shudihar R., British Guiana).

Length of male 14 mm, female 17 mm. Crown broadly rounded, three times as wide at base between eyes as median length.

Color: Head, pronotum and scutellum uniformly dull yellow (appears faded from a yellowish green). Forewings dark brown with many speckles of lighter brown and yellow.

Male genitalia: Pygofer rounded with two truncate apical lobes. Genital plate long, four times as long as wide, with rounded apex. Style with apical arm more than five times as long as wide, apex slightly expanded into a foot-like apex. Aedeagus with robust base, a pair of basal processes from base to ventral side of shaft, extending two thirds length of shaft; shaft tubular, ventral margin concavely depressed, six times as long as wide, expanded slightly at apex with two pair of subapical processes, outer pointed pair curved dorsad and laterad, inner bluntly rounded pair nearly paralleling shaft, gonopore apical.

Female genitalia: Seventh sternum (Fig. 7) more than twice as wide as median length; posterior margin excavated between rounded lateral lobes and median rounded projection, latter with slight median emargination.

Type: Holotype male, in the American Museum of Natural History Collection.

Notes: Other specimens seen are one male, GUYANA, Esseq., 6 mi. S. Wineperu, Picrewana Is., March 8–16, 1969, Duckworth & Dietz, and one female, GUYANA, Esseq., Plantain Is., March 25–26, 1969, Duckworth & Dietz, in the U.S. National Museum Collection. The holotype was used for the illustrations. The paratype male from Brazil was not seen, and can not be verified at this time as being this species.

Nancyana agitata sp. n.
(Figs. 3, 4, 13–17)

Length of male 15–15.5 mm, female unknown. Similar to *aldeia* in general size and color pattern, but with distinct male genitalia.

Male genitalia: Pygofer and genital plate (Figs. 16, 17) similar to *aldeia*. Style (Fig. 15) with apical arm more than 5 times as long as wide; apex expanded, foot-shaped, pointed at toe and heal. Aedeagus (Figs. 13, 14) with robust base; a pair of basal processes from base extending to ventral side of shaft, half way to apex of shaft; shaft tubular, ventral margin concavely de-

pressed, six times as long as wide, expanded slightly at apex with two pairs of subapical processes, outer pointed pair thicker at base, curving ventrad and laterad, inner bluntly rounded pair close to shaft, nearly same width to apex; gonopore apical.

Holotype male: VENEZUELA, Sn. Pedro de Cataniapo, T. F. Amazonas, 100 m, September 23–27, 1981, En la Luz, G. L. Garcia Coll., in the Universidad Central de Venezuela Collection. Paratypes: Two males, VENEZUELA, Bolivar, carret, Caicara, San Juan de Manapiare, KM 150, 300 m, March 21, 1978, Gadou Coll., one in the Universidad Central de Venezuela Collection and one in the University of Kentucky Collection.

Note: This species differs from the other known species of the genus by having the first pair of subapical processes of the aedeagus thicker at the base giving the outer margin a wavy appearance, and the second pair of subapical processes uniformly narrow and slightly longer than the first pair.

Nancyana isoclada sp. n.
(Figs. 18–22, 39)

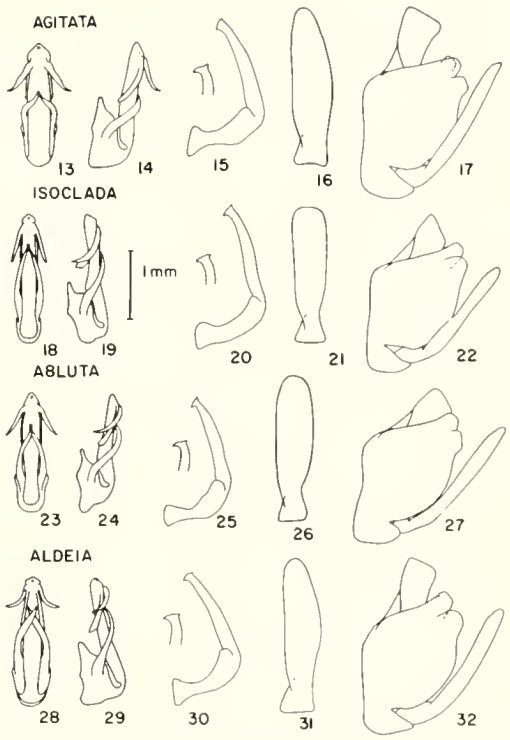
Length of male 13.5 mm, female unknown. Similar to *aldeia,* but slightly smaller and with distinct male genitalia.

Color: Head, pronotum and scutellum brown. Forewings brown, spotted with creamy brown overall and some darker brown spots in apical cells.

Male genitalia: Pygofer robust with apical margin with two truncate lobes, dorsal lobe longer. Genital plate three times longer than broad, apex broadest and truncate. Style long, with apex slightly expanded. Aedeagus with stout shaft with two pair of equally long subapical processes, outer pair pointed at apex, inner pair truncate at apex; base expanded with basal processes extending to two thirds length of shaft, bending to ventral side of shaft.

Holotype male: GUYANES, Ile de Touenké, 19–21-XI-1975, Itani (Guyanes) Mission, M. Boulard, P. Jauffret et P. Pompanon Coll., in the Muséum Paris.

Note: This species can be separated from the other known species of the genus by the subapical processes of the aedeagus being equal in length and both curving dorsad.

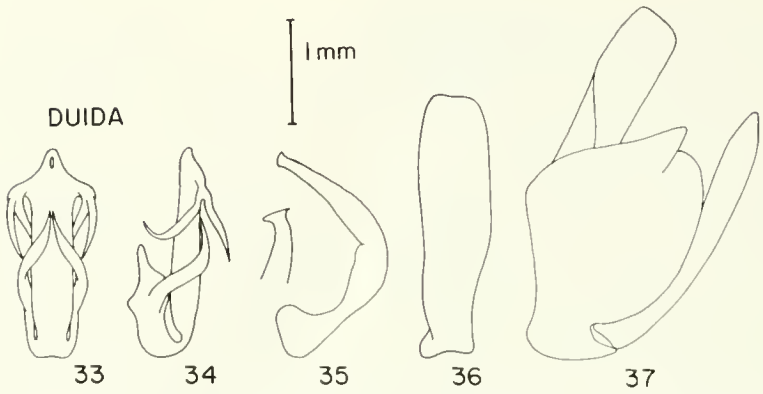


Figs. 13–17. *Nancyana agitata* sp. n. 13. Ventral view of aedeagus. 14. Lateral view of aedeagus. 15. Lateroventral view of style, with lateral view of apex. 16. Ventral view of genital plate. 17. Lateral view of genital capsule. Figs. 13–32 all drawn to the same scale.

Figs. 18–22. *Nancyana isoclada* sp. n. 18. Ventral view of aedeagus. 19. Lateral view of aedeagus. 20. Lateroventral view of style, with lateral view of apex. 21. Ventral view of genital plate. 22. Lateral view of genital capsule.

Figs. 23–27. *Nancyana abluta* sp. n. 23. Ventral view of aedeagus. 24. Lateral view of aedeagus. 25. Lateroventral view of style, with lateral view of apex. 26. Ventral view of genital plate. 27. Lateral view of genital capsule.

Figs. 28–32. *Nancyana aldeia* (DeLong). 28. Ventral view of aedeagus. 29. Lateral view of aedeagus. 30. Lateroventral view of style, with lateral view of apex. 31. Ventral view of genital plate. 32. Lateral view of genital capsule.



Figs. 33–37. *Nancyana duida* (DeLong). 33. Ventral view of aedeagus. 34. Lateral view of aedeagus. 35. Laterоventral view of style, with lateral view of apex. 36. Ventral view of genital plate. 37. Lateral view of genital capsule. All drawn to the same scale.

Nancyana abluta sp. n.
(Figs. 23–27)

Length of male 13.2 mm, female unknown. Similar to *isoclada,* but with distinct male genitalia.

Color: Head, pronotum and scutellum brown. Forewings brown spotted with creamy brown.

Male genitalia: Pygofer robust with apical margin with two truncate lobes, dorsal lobe slightly longer. Genital plate three times longer than broad, apex broadly rounded. Style long, with apex slightly expanded. Aedeagus with stout shaft with two pair of subapical processes, outer pair pointed, nearly same length as inner pair, apex curving dorsad, inner pair truncate at apex, paralleling shaft.

Holotype male: GUYANES, Antécumepata (Saut Kialo), 22-XI-1975, Itani (Guyanes) Mission, M. Boulard, P. Jauffret et P. Pompanon, in the Muséum Paris.

Note: This species can be separated from *isoclada* by the rounded apex of the genital plate and the subapical processes of the aedeagus not paralleling each other.

Nancyana gadouae sp. n.
(Figs. 8, 40)

Length of female 17.5 mm, male unknown. Similar to *aldeia,* except larger and with different shaped female seventh sternum.

Color: Head, pronotum and scutellum uniformly brown. Forewing dark brown speckled with lighter spots and apically with darker spots.

Female genitalia: Seventh sternum narrow, median lobe shorter than lateral lobes, with a slight median emargination.

Holotype female: VENEZUELA, S. [erranía] de Lema, 1200 m, V-1983, Gadou Leg., in the Universidad Central de Venezuela Collection.

Notes: This species is larger and darker in color than *aldeia* and the female seventh sternum is much narrower. This species is named after Mrs. Marilou Gadou, an excellent collector of Auchenorrhyncha.

Nancyana lubrica sp. n.
(Fig. 9)

Length of female 19 mm, male unknown. Similar to *aldeia,* but much larger and with a distinct seventh sternum.

Color: Head, pronotum and scutellum greenish brown, spotted with brown. Spots on pronotum appear as punctures. Forewings dark brown, heavily spotted overall with creamy brown, some blackish brown spots at apex.

Female genitalia: Seventh sternum with

median triangular lobe extending length of lateral lobes.

Holotype female: VENEZUELA, T. F. Amazonas, San Carlos de Rio Negro, 10-XII-1984, R. Brown Coll., in the Universidad Central de Venezuela Collection.

Note: This very large species is darker than other known species and the female seventh sternum is triangular instead of rounded.

Nancyana fernandezi sp. n.
(Fig. 10)

Length of female 17.5 mm, male unknown. Similar to *aldeia,* except larger and with a different shaped female seventh sternum.

Color: Head, pronotum and scutellum uniformly light brown. Forewings dark brown, heavily spotted with clear or creamy yellow spots.

Female genitalia: Seventh sternum with median lobe extending equal to lateral lobes, emarginate medially.

Holotype female: VENEZUELA, Bolivar, Km 107, El Dorado, Santa Elena, 520 m, 19-VIII-1957, F. Fernandez Y. & C. J. Rosales Colls., in the Universidad Central de Venezuela Collection.

Note: This species is named after the late Dr. F. Fernandez-Yepes an excellent entomologist and friend.

Nancyana fasciata sp. n.
(Figs. 11, 41)

Length of female 15 mm, male unknown. Similar to *aldeia* in size and color, but with a different shaped female seventh sternum.

Color: Head, pronotum and scutellum uniformly light brown. Forewings dark brown spotted and speckled with lighter and darker brown.

Female genitalia: Seventh sternum with a small rounded median lobe, shorter than lateral lobes, slightly emarginate medially.

Holotype female: VENEZUELA, Bolivar, El Bochinche, 200 m, 6–13-XII-1974, J. Salcedo and R. E. Dietz Colls., in the Universidad Central de Venezuela Collection.

Note: This species is very similar to *aldeia,* but the seventh sternum of the female is overall smaller with smaller lateral lobes.

Nancyana bordoni sp. n.
(Figs. 12, 42)

Length of female 17 mm, male unknown. Similar to *aldeia,* except larger, with darker markings on wings and a different female seventh sternum.

Color: Head, pronotum and scutellum uniformly light brown. Forewings dark brown, spotted with light brown basally, blackish brown apically, mostly shiny, appearing polished.

Female genitalia: Seventh sternum with a rounded median lobe as long as lateral lobes, slightly emarginate medially.

Holotype female: ARGENTINA, Pto. Iquazù, Misiones, 100 m, 25-XI–8-XII-1983, C. Bordon Coll., in the Universidad Central de Venezuela Collection.

Note: This species is named for Dr. Carlos Bordon, a well-known entomologist and the collector of this species.

Nancyana curva sp. n.
(Fig. 43)

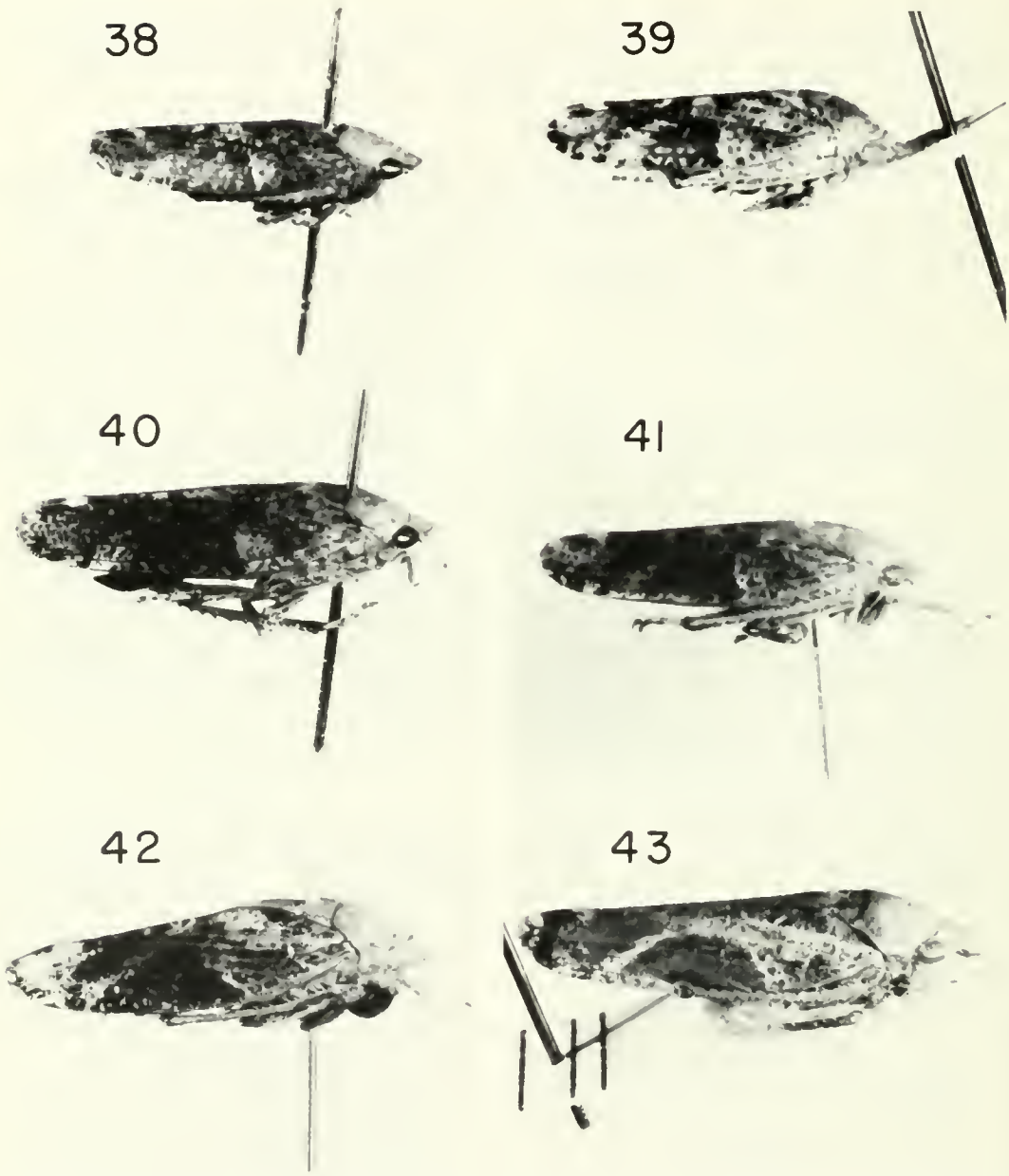
Length of female 16.5 mm, male unknown. Similar to *aldeia,* except larger, with a distinct color pattern and different female seventh sternum.

Color: Head, pronotum and scutellum uniform light brown. Forewings brown spotted with creamy yellow or white, with a large solid brown half circle area near middle along costal margin, and darker blackish brown spots in apical cells.

Female genitalia: Seventh sternum similar to *aldeia* in shape, except median lobe extending beyond length of lateral lobes.

Holotype female: GUYANE, Riviere-Camopi, Mont Alikene, 11-XI-1969, Piége Lumineux, Guyane Mission, Balachowsky-Gruner, Oct.–Nov. 1969, in the Muséum Paris.

Note: This species is easily separated from the presently known species of this genus by the very distinct brown half-circle on the forewing, whereas in most species the fore-



Figs. 38–43. *Nancyana* spp., lateral view. 38. *N. aldeia* (DeLong), male from Guyana. 39. *N. isoclada* sp. n., holotype. 40. *N. gadouae* sp. n., holotype. 41. *N. fasciata* sp. n., holotype. 42. *N. bordoni* sp. n., holotype. 43. *N. curva* sp. n., holotype. Length of each given in species description, approximately 2×.

wings are just generally spotted and speckled with only a slight pattern.

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thank R. T. Schuh, American Museum of Natural History for the loan of the type material. This paper is published with the approval of the Director of the Kentucky Agricultural Experiment Station as journal article no. 89-7-202.

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92(3), 1990, pp. 538–543

THE GENUS *XIPHOGRAMMA*, ITS OCCURRENCE IN NORTH AMERICA, AND REMARKS ON CLOSELY RELATED GENERA (HYMENOPTERA: TRICHOGRAMMATIDAE)

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Abstract.—The genus *Xiphogramma* is briefly reviewed and compared to related genera, *Chaetogramma* and *Brachygrammatella*. ***Xiphogramma fuscum*** n. sp., the first species from the New World, is described from southwestern North America. A key to the species of *Xiphogramma* and a description of the male genitalia are included.

Key Words: Hymenoptera, Trichogrammatidae, *Xiphogramma* taxonomy

The genus *Xiphogramma* Nowicki, with three species included, has been known only from the Old World (Doutt 1974, Hayat 1980). This paper describes a fourth species, from North America, and includes a key to the known fauna. The characters of the new species indicate the artificiality of *Chaetogramma* Doutt, as defined by Hayat (1981). Arguments for and against synonymy of these genera are presented.

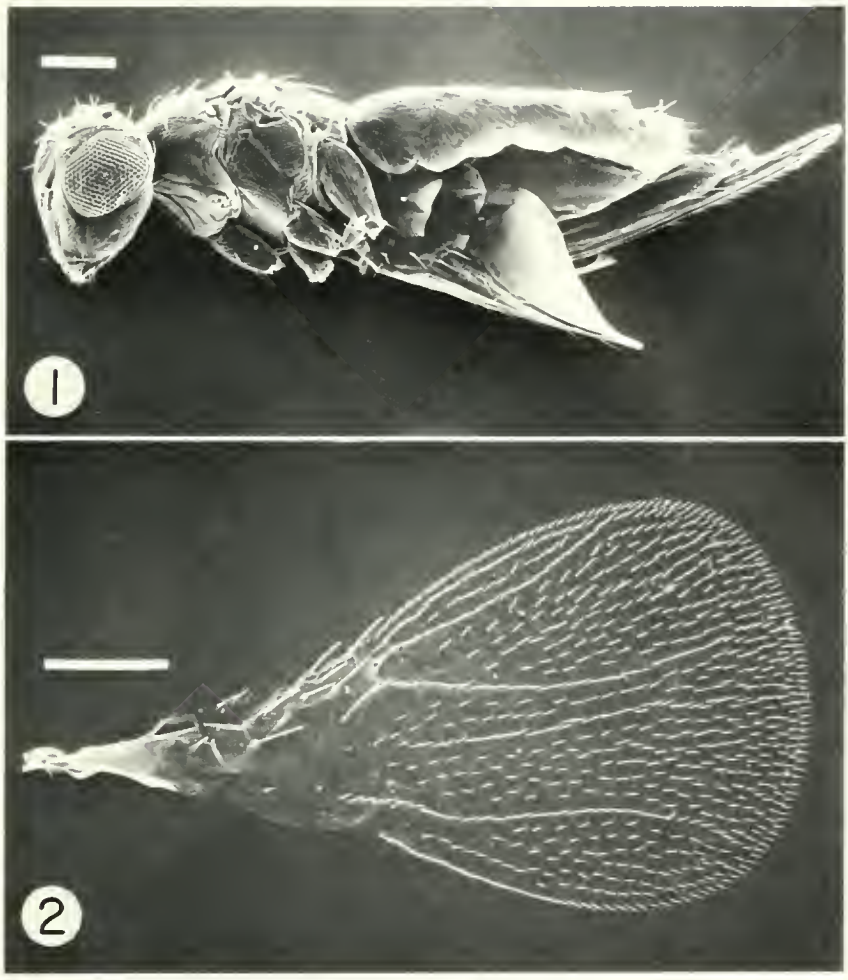
Hosts of *Xiphogramma* are unknown. The species described here emerged from grape leaves containing eggs of both Cicadellidae and Miridae. Of its related genera, *Chaetogramma* and *Brachygrammatella* Girault, hosts of only the latter are known. Species of *Brachygrammatella* have been associated with eggs of Cicadellidae, Membracidae and Miridae (Doutt 1968, Viggiani 1968, Yousuf & Shafee 1987).

Xiphogramma

Xiphogramma was described by Nowicki (1940) for the unique European trichogrammatid, *X. holorhoptra* Nowicki. He afforded the species generic status on the basis of ovipositor structure—"abdomen with a powerful ovipositor occupying its entire length and protruded for more than a half of abdomen's length: the valvae are much broadened before the tip, curved upwards and sabre-like." All *Xiphogramma* species have an exserted, curved ovipositor, but it is not necessarily as long as in *X. holorhoptra*.

Other features of the genus include antenna with two anelli, two subequal, closely-appressed funicle segments, one-segmented club, club not widest at base; maxillary palp one-segmented; vertex wrinkled, vaulted; wing disk densely setate, vein tracks, if present, usually becoming obsolescent apically; stigmal vein broad, subsessile, marginal vein not densely setate; a dark macula of varying size and intensity beneath venation; tarsal segment I of middle leg elongate, distinctly longer than that of hind leg.

An African species, *X. anneckei*, was added by Doutt (1974), and *X. indicum*, from India, was described by Hayat (1980). The new species described below occurs in arid and semiarid regions of southwestern North America. Males and females have been collected. Heretofore, the only male of *Xiphogramma* known was the allotype of *X. anneckei*.



Figs. 1, 2. *Xiphogramma fuscum*, female. 1, Lateral view (appendages removed). 2, Forewing. Scale bar = 0.1 mm.

Xiphogramma fuscum, New Species

The description is based on critical point dried (for color and body length measurements) and slide mounted specimens. Quantitative data represent means taken from three specimens from the type locality; the mean is followed by a range, in parentheses, if variation is considerable. Significant intraspecific variation among locales was not detected.

Female (Fig. 1).—Body length 1.08 mm; 0.95 mm excluding exserted ovipositor.

Color: Primarily dark brown except as follows: head with linear yellow area along medial rim of eye; frons yellow brown; face yellow brown to dark brown. Antenna with scape primarily pale yellow, margined with brown; pedicel light brown; funicle yellow brown; club pale brown or yellow brown. Thorax with narrow linear yellow marking at midline of pronotum and immediately lateral to mid-lobe of mesoscutum; mesepimeron, mesepisternum with at least some yellow; metanotum, propodeum, segment I of gaster yellow except laterally. Legs brown except apex of coxae, trochanters, base and

apex of femora and tibiae, and tarsi whitish (apical tarsal segment may be pale brown). Venation of fore wing bicolored; stigmal vein, apical half of marginal vein pale brown; remainder of venation pale yellow. Wings hyaline except a small fumate area beneath stigmal vein.

Head: Length and width subequal; vertex vaulted, arched above eyes, wrinkled; scrobes relatively deep; lower margin of torulus coincident with ventral margin of eye; malar space ca. 0.6 eye length. Mandible with four teeth.

Antenna (Fig. 3) with second anellus very short, inconspicuous, closely appressed to funicle; F1, F2 subequal in length; length/width of segments as follows: scape—3.42, pedicel—2.07, F1—0.62 (0.58–0.67), F2—0.74 (0.71–0.78), club—2.29 (2.2–2.4); antenna moderately setate, setae longer, stouter on pedicel and funicle; F1 with 1 transverse placoid sensillum, distal portion of sensillum curved toward apex of segment; F2 with 3 oblique placoids; F1, F2 each with several basiconic peg sensilla on apical margin; club with 12 linear placoids, club also with many thin-walled setiform sensilla at apical half and several basiconic peg sensilla near middle.

Thorax: Forewing (Fig. 2) broad, suboblate apically, 0.55 as broad as long, with a very short fringe; venation attaining 0.43 length of wing; setation on disc apical to venation dense; vein tracks becoming obsolescent apically; RS_1 represented by 2–3 setae, 2 setae in line with RS_1 on apex of stigmal vein; basal vein track with 2 setae; costal cell, narrow, with setae along apical half of anterior margin; relative length of veins as follows: subcostal—29, premarginal—14, marginal—15, stigmal—6; marginal vein stout, slightly, gradually widened apically with about 8 setae; stigmal vein poorly defined, stout, subsessile, ca. as long as broad; premarginal vein with 2 setae; subcosta with 1 seta at middle. Hindwing moderately broad, maximum width of disk 1.4× length of longest posterior fringe setae; with 2 distinct setal tracks just behind anterior margin, remainder of disk with many scattered setae.

Thoracic setae elongate, stout; mid-lobe of mesoscutum with 4 setae of subequal length; scutellum with posterior pair of setae ca. 1.5× as long as anterior pair; lateral lobe of mesoscutum, axilla each with 1 elongate seta.

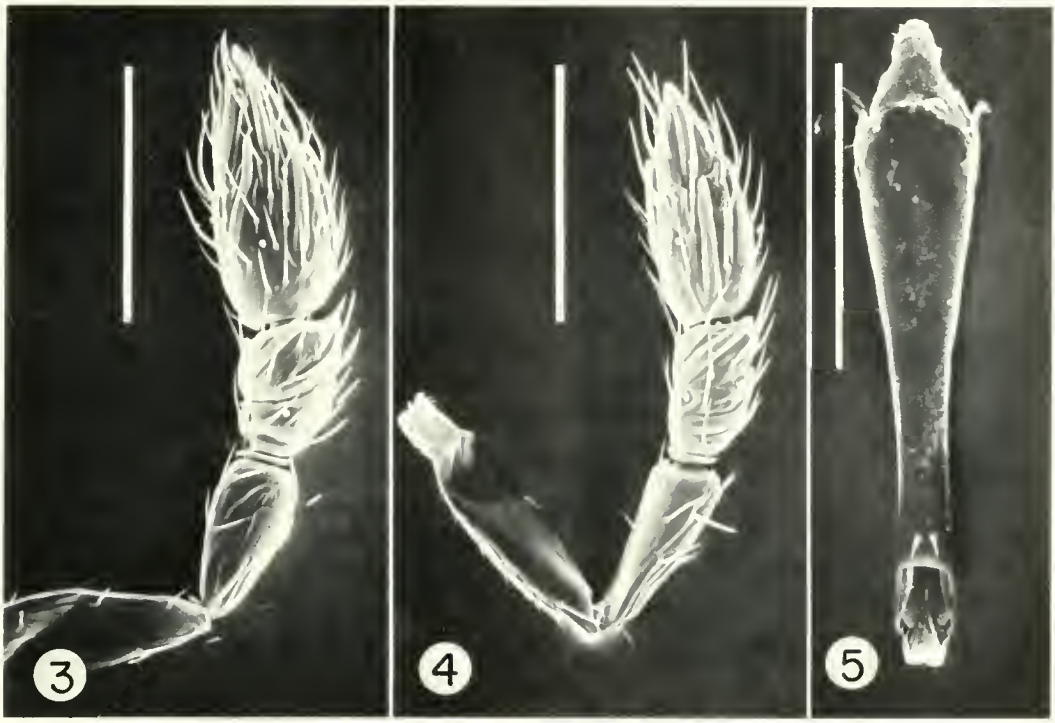
Foretibia with 5 "teeth" on anterior surface, basal 2 weaker than apical ones. Fore and middle femora with a relatively elongate seta ventroapically. Hind femur distinctly broader than others; hind trochanter swollen dorsally. Tibial spurs not plumose. Relative length of coxae, trochanters, femora, tibiae, and (tarsi) as follows: fore leg—26:11:41:32:(9:11:11); middle leg—21:14:40:49:(19:14:13); hind leg—35:17:40:48:(13:13:13); length of apical tibial spines 4, 7, 8, resp.; length of apical setae on fore and middle femora 8, 11, resp.

Gaster (Fig. 1): Gaster (excluding ovipositor) elongate, apically acuminate, ca. 1.5× as long as thorax; hypogynium attaining 0.8 length of gaster. Ovipositor elongate, running along entire length of gaster and beyond, broadly curved dorsally, its length 2.6–3.1 length of mid and hind tibiae; gonoplac elongate, densely setate, comprising 0.36 length of entire ovipositor, almost its entire length extending beyond apex of gaster; gonangulum small, subtriangular, basal 0.10 of ovipositor extending anterior of gonangulae.

Male.—As in female except as follows:

Head (in 3 of 6 dried specimens) paler with vertex yellow lateral and dorsal to scrobes. Antenna (Fig. 4) with pedicel, F1 more elongate; with only 1 placoid sensillum on F2, 5 placoids on club; club segments incompletely fused, an obsolescent U-shaped suture on anterior surface between basal and apical placoids; length/width of segments as follows: scape—3.50, pedicel—2.41, F1—1.07, F2—0.75, club—2.19.

Genitalia (Fig. 5) very similar to that described for *Chaetogramma maculata* (Hayat 1981, Fig. 5); very elongate, narrow,



Figs. 3–5. *Xiphogramma fuscum.* 3, Right female antenna (anterior surface). 4, Right male antenna (same). 5, Male genitalia (ventral). Scale bar = 0.1 mm.

6.7× as long as wide, length subequal to that of hind tibia; aedeagus fused to genital capsule, apodemes absent; base of genital capsule attenuate, its ventral region extending anteriorly; posterior border of anterodorsal aperature not sclerotized, poorly indicated; genital capsule with 2 short, stout spines apicoventrally; volsellae broad, unarmed, apically truncate; gonostyli not differentiated.

Types.—Holotype female; from Mexico, Sonora, Caborca; emerging in laboratory from grape leaves collected 2-VI-1989; L. Drake, collr.; deposited in the United States National Museum. Allotype male; same data as holotype; deposited in the United States National Museum. Additional specimens from Caborca (4 ♀♀, 7 ♂♂) are designated paratypes and deposited as follows: 1 ♀, 1 ♂, British Museum (Natural History); 1 ♀, 1 ♂, Canadian National Collection (Ottawa); 2 ♀♀, 5 ♂♂, University of California (Riverside). The holotype, allotype and 6 of the paratypes (3 ♀♀, 3 ♂♂) are mounted on glass slides in Canada balsam. One ♀ and 4 ♂♂ paratypes are card mounted.

Diagnosis.—*X. fuscum* is similar to *X. indicum.* Characters separating them are presented in the key below. The most similar species in North America is *Chaetogramma occidentalis* Doutt. Ovipositor length (short, not exserted in *C. occidentalis*) separates females. Genital structure will distinguish males. In *X. fuscum,* the aedeagal apodemes are not expressed and the base of the genital capsule is attenuate anteriorly (Fig. 5); in *C. occidentalis* the apodemes are well developed, and the genital capsule is truncate basally (Pinto, unpubl.). Also in *X. fuscum* the two funicle segments are distinct and not partially fused as in *C. occidentalis.*

Etymology.—The specific name is Latin and refers to the dark brown body color.

Host.—The host of *X. fuscum* is unknown. Specimens from Caborca, Sonora, and Tonopah, Arizona, emerged from grape

leaves harboring eggs of leafhoppers and mirid bugs (*Parthenicus*).

Records.—19 ♀♀, 12 ♂♂. MEXICO. *Baja California Sur:* Ciudad Constitucion, 11 km N.; 1 ♀; 27-X-1983; screen sweeping desert vegetation; J. D. Pinto. *Sinaloa:* Mazatlan, 12 mi. N.; 1 ♀; 25-X-1982. *Sonora:* Caborca; 5 ♀♀, 8 ♂♂; emerging from grape leaves coll. 2-VI-1989, 27-VII-1989 & 2-VIII-1989; L. Drake. Hermosillo; 1 ♀, 1 ♂; emerging from grape leaves coll. 2-VI-1989, 9-VII-1989; L. Drake; & 4 ♀♀; 6-X-1985; D. Gonzalez. UNITED STATES. *Arizona:* Stanfield, 1 ♀, emerging from grape leaves coll. 11-VII-1989; L. Drake. Sycamore Canyon, 9 mi. W. Peña Blanca Lk. (Santa Cruz Co.), 4100 ft. elev.; 1 ♀; 12-VII-1983; R. Anderson. Tonopah; 1 ♀, 1 ♂; emerging from grape leaves coll. 21-VI-1989; L. Drake. *California:* Baker, 11 km N.; 1 ♀; 30-III-1989; screen sweeping desert vegetation; J. D. Pinto. Hemet, E of (4000 ft. elev.); 1 ♀; screen sweeping *Adenostoma sparsifolium* Torr.; 30-VI-1983; R. Velten. *Texas:* Ben Bolt, 8 mi. W. (La Copita Res. Sta.); 3 ♀♀, 2 ♂♂; 20-V-1987; screen sweeping; J. B. Woolley.

Key to the Species of *Xiphogramma* (Females)

1. Gaster elongate, its length at least 2× that of thorax; exserted portion of ovipositor greater than half gaster length 2
– Gaster shorter, its length about 1.5× that of thorax, subequal to length of head and thorax combined; exserted portion of ovipositor not greater than half gaster length 3
2. Dorsum of gaster primarily dark brown, weakly marked with yellow at tergal margins only. Marginal vein widened apically. Length of funicle equal to or slightly shorter than pedicel. Europe (Poland) ..... *X. holorhoptra*
– Dorsum of gaster primarily yellow, marked with brown; marginal vein not widened apically. Length of funicle distinctly greater than that of pedicel. Africa (South Africa, Tanzania, Ivory Coast) ..... *X. anneckei*
3. Hypogynium elongate, attaining apex of gaster. Antenna with F1 as long as or longer than wide, longer than F2. India ..... *X. indicum*
– Hypogynium shorter, attaining 0.8 gaster length. Antenna with F1 distinctly wider than long, subequal in length to F2. Southwestern North America ..... *X. fuscum*, n. sp.

Discussion

Xiphogramma is closely related to *Brachygrammatella* and *Chaetogramma*. Wing and antennal structure is similar in all three genera.

Brachygrammatella is distinguished by the densely setate marginal vein, and minor antennal differences (club widest at base, funicles much broader than long); also, the ovipositor in this genus does not project beyond the gaster (see Doutt and Viggiani 1968).

Doutt (1974) described *Chaetogramma* for an African and a North American species, which he separated from *Xiphogramma* primarily by the short ovipositor (not extending beyond gaster), and the fused or partially fused funicle segments. His statement that the number of anelli also separate the two (1 in *Chaetogramma*, 2 in *Xiphogramma*) is incorrect. There are 2 anelli in both, as well as in *Brachygrammatella*.

Hayat (1981) divided *Chaetogramma* into two subgenera, the nominate, which includes both of Doutt's species, and *Chaetogrammina*, erected for *C. maculata* Hayat from India. *Chaetogrammina* was distinguished primarily by its completely divided funicle segments, its more distinct vein tracks and better developed costal cell. Male genitalia, not compared by Hayat, provide another difference. In the nominate subgenus distinct aedeagal apodemes are present (Pinto, unpubl.) as they are in *Brachygrammatella* (Viggiani 1971, Pinto, unpubl.). In *Chaetogrammina*, based on descriptions and figures in Hayat (1981) and Viggiani (1984), they are absent or poorly developed.

Viggiani (1984) pointed out the similarity of male genital structure in *Brachygrammatella* and *C.* (*Chaetogrammina*) and, on this basis, questioned the validity of *Chaetogramma*. The male genitalia in *Xiphogramma* cast further doubt on the validity of *Chaetogramma*. They are virtually identical to that in *C.* (*Chaetogrammina*) *maculata*.

The only character now separating *Xiph-*

ogramma and *Chaetogramma* is ovipositor length. The difference in length between *X. anneckei* and *X. holorhoptra* on the one hand, and species of *Chaetogramma* on the other, although considerable, is bridged substantially by *X. indicum* and *X. fuscum*. For example, in *X. anneckei* the exserted portion of the ovipositor is 0.8–0.9 the length of the gaster, and in *C. maculata* the ovipositor does not extend beyond the gaster. In *X. fuscum*, however, the exserted portion of the ovipositor is never more than 0.45 gaster length. Although synonymy is suggested, I hesitate at present for the following reason. *Chaetogramma*, as currently defined, is paraphyletic. It is distinguished from *Brachygrammatella* and *Xiphogramma* only by primitive traits (e.g. absence of a densely setate marginal vein, and a short ovipositor). Synonymizing it with *Xiphogramma* simply results in a larger paraphyletic unit, more difficult to characterize than either is at present.

Structure of the forewing, antenna and genitalia suggest that *C.* (*Chaetogrammina*) is closer to *Xiphogramma* than to its nominate subgenus. Moving this subgenus to *Xiphogramma* probably is appropriate. The only clearly derived traits currently justifying this are associated with the male genitalia, however. Because the male genitalia are known in only one species of *Xiphogramma*, I consider it premature to transfer *Chaetogrammina* and then define *Xiphogramma* solely on male features.

Acknowledgments

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OCCURRENCE OF SEXUAL MORPHS OF RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (HOMOPTERA: APHIDIDAE), IN SEVERAL LOCATIONS IN THE SOVIET UNION AND THE NORTHWESTERN UNITED STATES

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Abstract.—*Diuraphis noxia* were collected in North America and the Soviet Union during autumn 1989. Sexual forms constituted more than half of Moldavian and Crimean collections and about nine percent of collections near and between Odessa and Kherson, Ukraine. Six oviparae were found in Idaho and Oregon, but they represented less than 1 percent of total collections. No sexuales were found in the Soviet Republic of Kirghizia. Moldavian *D. noxia* colonies readily produced sexual forms under natural autumn conditions, whereas an Idaho isolate of *D. noxia* produced no males or oviparae after 10 weeks under a 6:18 (L:D) photoperiod at 10°C. Under a photoperiod of 8:16 (L:D) at 20°C, Moldavian *D. noxia* produced sexual forms, but Syrian, French, Turkish, Jordanian and Kirghizian populations did not. A Kirghizian population did produce sexuales and eggs at 16°C and a photoperiod of 14:10 (L:D).

Key Words: *Diuraphis noxia,* Aphididae, sexuals

There are two overwintering strategies among Aphididae. Some populations (termed holocyclic) produce males and oviparae which must mate to produce viable overwintering eggs. Other populations (termed anholocyclic) overwinter in protected locations as viviparous females, and no sexual morphs are produced. Some populations can utilize either strategy depending upon climatic conditions.

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), a serious pest of small grains, is indigenous to the Middle East, the Soviet Union, Afghanistan and probably western China (Hewitt et al. 1984). Holocyclic populations of *D. noxia* are known from the Soviet Union (Grossheim 1914). Sexual forms have been described briefly by Grossheim (1914), but no formal descriptions exist. On 7 IX 1989, Dr. Manya B. Stoetzel found an apterous male in a laboratory colony maintained at the USDA-ARS European Parasite Laboratory, Behoust, France, and originally collected in Kishinev and vicinity, Moldavia, USSR, 28 V–2 VI 1989 on wheat and barley by Dr. Tad Proprawski and Françis Gruber (M. B. Stoetzel, personal communication). Additional males

[1] Order reprints from Susan Halbert.

and oviparae have been obtained from this colony. *Diuraphis noxia* was recently introduced into South Africa and North America (Stoetzel 1987, Walters 1984). Prior to this article, no sexual forms of *D. noxia* have been reported from North America, although *D. noxia* has been reported as far north as 50° latitude in Canada (Jones et al. 1989). No sexual forms have been reported from South Africa.

The purpose of the surveys was to compare occurrence of the various morphs of *D. noxia* in the northwestern United States and the Soviet Union where *D. noxia* is native. Our preliminary attempts to force various populations of *D. noxia* to produce sexuales under laboratory conditions are presented here to support field observations and are not intended to be definitive experiments on the nature of triggering mechanisms for development of sexuales.

Methods

Live *D. noxia* were collected on wheat and barley from two fields in Moldavia (October 25–27, 1989), four fields in the Crimean Peninsula (October 31–November 2, 1989), five fields in the southern Ukraine (near and between Odessa and Kherson) (November 2–4, 1989), seven fields in the Kirghiz Inner Tian Shan Range of south central USSR (September, 1989), six fields in the Treasure Valley of Canyon County, Idaho and Malheur County, Oregon (November 14–16, 1989) and 2 fields in the Palouse area of Latah and Nez Perce Counties, Idaho (November 25–27, 1989). In the Ukraine and Moldavia *D. noxia* is quite rare, so every colony found was collected. In the Treasure Valley where *D. noxia* is more abundant, infested plants were selected along a 100 m transect within each field, and additional plants were collected in heavily infested areas of several fields. In the Palouse area, wild oat plants with obvious damage symptoms along the perimeter of a field previously in barley (Latah County) and within a winter wheat field (Nez Perce County) were collected. In Kirghizia, heavily infested wheat and barley plants were selected. In the Soviet Union and the Treasure Valley, immature aphids were kept on fresh wheat plants in plastic containers until they became adults. Nymphs with wing pads which died before reaching maturity were recorded as alatae. Other nymphs which died prior to reaching maturity were recorded as undifferentiated nymphs. Adult aphids were examined and preserved in 70% ethanol. In the Palouse, only adults were examined. Voucher specimens are on deposit at the All Union Research Institute for Biological Methods in Agriculture, Kishinev, Moldavia, U.S.S.R.; the USDA European Parasite Laboratory, Behoust, France, the University of Idaho Southwest Idaho Research and Extension Center, Parma, Idaho, U.S.A.; the Pasteur Institute, Paris, France; and the USDA-ARS Systematic Entomology Laboratory, Beltsville, Maryland, U.S.A.

In preliminary experiments, we have made attempts to force various populations of *D. noxia* to produce sexual morphs by subjecting them to short days and cool temperatures (Blackman and Eastop 1984). In Idaho, one of us (S.H.) maintained North American *D. noxia* individually in petri dishes supplied regularly with fresh leaves on moist cotton subjected to a photoperiod of 6:18 (L:D) at 10°C from February–April, 1988. A similar experiment was done at the USDA-ARS European Parasite Laboratory, Behoust, France using Moldavian, Syrian, Jordanian, French, Turkish and Kirghizian *D. noxia* kept at a photoperiod of 8:16 (L:D) at 20°C from October–December, 1989 (F.G. and T.P.).

Results and Discussion

Collections in the USSR.—No alatae or alatoid nymphs were found in the Ukraine or Moldavia (Table 1). In Moldavia all 26 of the adult *D. noxia* found or reared were oviparae. In the Crimean Peninsula, the only location where males were found, four fifths

Table 1. Morphs of *Diuraphis noxia* (Mordvilko) found in 6 locations in the southern Soviet Union and northwestern United States. 1989.

Location	Month of Collection	Number of Sites	Morphs Found				
			Alate Viviparae[1]	Apterous Viviparae	Oviparae	Males	Undifferentiated Nymphs[2]
Moldavia	October	2	0	0	26	0	1
Crimea	November	4	0	6	21	3	6
Ukraine[3]	November	5	0	89	9	0	0
Kirghizia	September	7	76	843	0	0	43
Treasure Valley[4]	November	6	107	401	5	0	70
Palouse	November	2	8	193	1	0	—[5]

[1] Includes alatoid nymphs in Treasure Valley collections.
[2] Aphids collected were maintained in cages to allow them to become adults before they were scored. Nymphs without wing pads which died before becoming adults are scored as undifferentiated nymphs.
[3] Fields near and between Odessa and Kherson.
[4] Fields in Canyon Co., Idaho and Malheur Co., Oregon.
[5] Fields in Latah and Nez Perce Counties, Idaho. Only adults were counted.

of the 30 adult aphids recovered were sexual forms (21 oviparae, 3 males). In the southern part of the Ukraine 9 of the 98 adult *D. noxia* recovered were oviparae. No sexuales were found in Kirghizian collections.

Diuraphis noxia is not common in Moldavia or the Ukraine in the autumn and is not considered an important pest. The infestations we observed affected isolated plants or patches up to 2 m in diameter. *Diuraphis noxia* was most common in volunteer grain. In winter wheat, infestations were found most often near field borders or in places where plants were relatively sparse. Plants showing characteristic *D. noxia* damage typically had one or two *D. noxia*. Other cereal aphids, particularly *Rhopalosiphum padi* (L.), *Rhopalosiphum maidis* (Fitch) and *Sitobion avenae* (Fabricius), were common. In North America and Kirghizia, *D. noxia* is much easier to find, and infested plants often have large colonies of aphids.

Collections in North America.—It was surprising to find oviparae in the Treasure Valley and the Palouse in Idaho and Oregon. In all, 6 oviparae were found from two fields in the Treasure Valley and one field in Latah Co., Idaho among 785 *D. noxia* examined from a total of 8 fields. No males have been found to date, but the presence of oviparae opens the possibility that a small percentage of the North American *D. noxia* population is now holocyclic. Males, which were much less common than oviparae in the Soviet Union, may have been overlooked in our limited North American collections. The fact that oviparae were found in several fields in Idaho and Oregon increases the possibility that an occasional male could find a mate. The unusually harsh winter of 1988/9 in the Pacific Northwest USA could have provided a heavy selective advantage to holocyclic populations which resulted in their reaching detectable levels this year.

Another possible explanation for the presence of oviparae follows from Blackman (1974). He has reported clones of *Myzus persicae* (Sulzer) which he terms androcyclic because they produce occasional males but no oviparae. Similarly, it is possible that North American *D. noxia* are gynocyclic, occasionally producing oviparae but not males.

Preliminary laboratory experiments.—North American *D. noxia* subjected to a photoperiod of 6:18 (L:D) at 10°C for 10 weeks produced no sexual morphs. Syrian, Jordanian, French, Turkish and Kirghizian *D. noxia* produced no sexual morphs after three months at a photoperiod of 8:16 (L:D) at 20°C, but a Moldavian population kept

under the same conditions produced oviparae, males and eggs. A Moldavian population collected in August, 1989, and propagated under natural autumn conditions produced abundant sexuales and eggs by 23 October. Surprisingly, a Kirghizian population maintained for two months at 16°C and a photoperiod of 14:10 (L:D) at the European Parasite Laboratory produced sexuales and eggs. More research is needed on mechanisms for triggering production of sexuales in *D. noxia*.

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SCALE-LIKE STRUCTURES ON THE TIBIA OF THE PARASITIC WASPS, *TRICHOGRAMMA* SPP. (HYMENOPTERA: TRICHOGRAMMATIDAE)

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Abstract.—Nine scale-like structures were found at the distal end of the hind tibia in both sexes of *Trichogramma.* No pore can be detected in these structures and they are so thin that they appear transparent. Behavioral observations indicate that they are probably used as brush to transfer a secretion from the abdomen to the wings to keep them from drying and thus increases the aerodynamic function of the wings, or it might be that some unknown behavioral semiochemical is transferred to the wing.

Key Words: SEM, morphology, behavior, aerodynamic, semiochemical

A scale-like structure in the parasitic wasps, *Trichogramma* spp., was first reported by Hung at the First International Symposium on *Trichogramma* and Other Egg Parasites in 1981 (Hung 1982). This unique structure was subsequently found in other *Trichogramma* by Cals and Cals-Usciati (1987) and Schmidt and Smith (1987). However, none of these papers gave a detailed description. Since this structure has never been observed in any other group of insects, further description and discussion are given here.

MATERIALS AND METHODS

Seven species of *Trichogramma* were used in this study, namely *T. exiguum* Pinto and Platner, *T. maltbyi* Nagaraja and Nagarkatti, *T. minutum* Riley, *T. nubilale* Ertle and Davis, *T. parkeri* Nagakatti, *T. pretiosum* Riley, and *T. stampae* Vincent. *Heliothis virescens* (F.) eggs killed by exposure to ca. 30 krad of gamma radiation were used as the host in rearing the cultures. All cultures were maintained individually in 10-dram plastic vials at 27°C, 70–80% relative humidity.

Live wasps were fixed in chilled 3% glutaraldehyde for 3 h at room temperature and dehydrated through 100% ethanol. They were then critical point dried, mounted on stubs with silver paint and coated with gold/palladium alloy. The specimens were studied with both Hitachi S-430 and Hitachi HHS-2R scanning electron microscopes at an accelerating voltage of 15 and 20 kV. Specimens freshly killed with CO_2 can also be mounted directly on stubs with TV tube coat and studied at 15 kV without gold/palladium coating for up to one hour before they collapse. Behavioral observation was carried out under WILD M5D stereomicroscope.

RESULTS AND DISCUSSION

Nine scale-like structures were found in both sexes of all seven species studied. They are located on the inner surface at the distal end of hind tibia (Fig. 1). Six of them form a half-ring around the tarsal socket (Fig. 2). The 7th scale is located about 5 micra above the ring, in line with the tibial spur (sp). The remaining two are on the same line between scales 6 and 7. Scale 9 is about 15 micra

above the ring with 8 about half-way in between. Each scale is socketed. Their dimensions are 10–19 micra in length, 2.5–7.6 micra in width and 0.16–0.5 micra in thickness, with #1 the largest and #9 the smallest in size. Each scale is corrugated on both sides (Fig. 3) and keeled underneath (Fig. 2). No pore can be detected even at 20K magnification. Each scale is so thin that it can be seen through when two scales are partially overlapped (Fig. 4). The thinness of this structure has caused problems in studying it under SEM, because the tip can readily curve up under the electron beam even at 15 kV with metal-coated specimens.

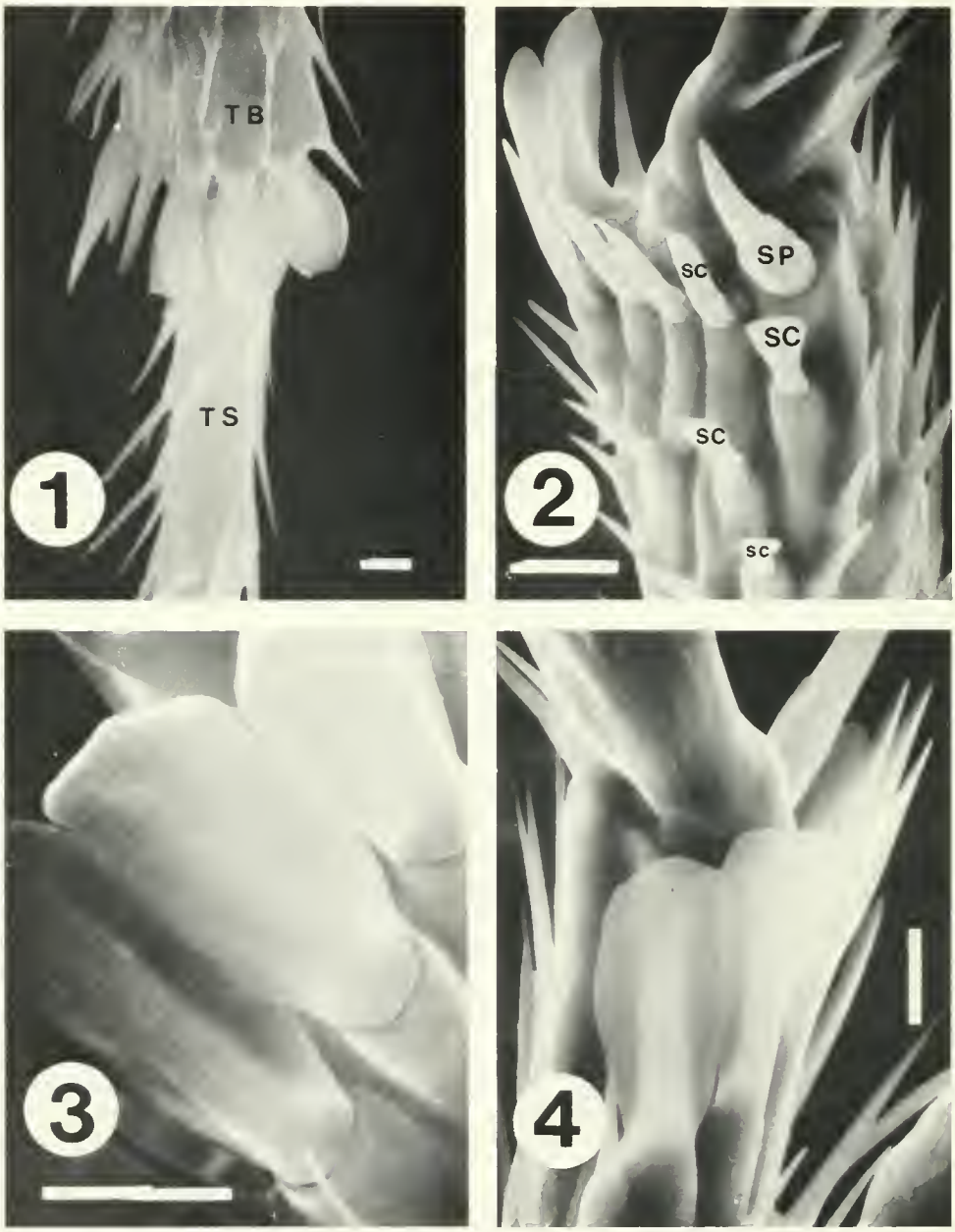
Rosen and DeBach (1976) reported the presence of strigil on fore leg and saltatorial mid-tibial spur in *Aphytis chilensis* Howard. However, they did not mention any scale-like structure. Despite the size of these scales in relation to the tarsal segment (see Fig. 1), they cannot be clearly detected with the phase contrast microscope in slide preparations even when mounted in glycerine or distilled water. Under both compound and stereo microscopes, only what appear to be setae at the apex of the tibia can be seen to have an arrangement very similar to that of these scale-like structures. Under stereomicroscope, if the position of the leg or the light source is manipulated at various angles, a thin membrane can be detected around these "setae." Therefore, it is apparent that these structures are so thin and transparent that they cannot be discerned under light microscopes and only the middle ridges can be seen which have the appearance of setae.

Cals and Cals-Usciati (1987) briefly described these structures in *T. maidis* Pintureau and Voegele. They also reported the occurrence of "similar" structures on the pretarsus which they called "scraping setae." However, these "linear serie (sic) of scraping setae" are not "petal-like" as originally reported by Hung (1982). Schmidt and Smith (1987) also found the same structure in *T. minutum* in their SEM study. According to them, there are eight flattened and grooved modified hairs that form a wing comb at the distal rim of the metatibia; the outer surface of each hair is marked with four to five sculpted ridges and the inner surface is smooth (Schmidt and Smith 1987). However, as pointed out by Hung (1982), there are nine such structures (see Fig. 2). Furthermore, each scale is corrugated on both sides with more than 10 ridges and keeled underneath (Figs. 2, 3). Whether these differences reflect variations not observed previously cannot be confirmed at this stage.

The lack of any pores rules out the possibility that they are chemoreceptors. It is possible that the pores may be very small and not visible at the resolution and magnifications used in this study. However, the use of higher magnification will certainly be very difficult, if not impossible, because these structures can readily be deformed under the electron beam. They could be mechanoreceptors which are stimulated when the legs touch the abdomen or ovipositor. However, it is hard to understand why such mechanoreceptors need to be shaped like scales.

Many species of insects communicate with each other by tapping their antenna or feet against the bodies of other insects. Radiation from thin layers of molecules coated in insect bodies can be modulated by this tapping (Callahan 1977). The thinness and corrugations of these scale-like structures on the hind leg might be used for the impedance match for some incoming far IR radiation, possibly from some host oscillating molecule (P. S. Callahan, per. comm.).

The function of this structure can only be speculated, based on my observation of the behavior of this wasp. Both male and female *Trichogramma* frequently rub the legs against the abdomen and the wings. It is this particular part of the leg where the scales are located that is used in this abdominal stroking and wing brushing. Although they also rub the legs against each other, only the tarsal segments are involved. It is, therefore,



Figs. 1–4. The scale-like structure in *Trichogramma* spp. 1. *T. exiguum* female, hind tibia (TB) and tarsus (TS) with the scales. 2. *T. stampae* female, distal end of hind tibia (pointing upward) showing nine scales (SC) and the spur (SP). 3. *T. maltbyi* female, the corrugated surface of the scale. 4. *T. nubilale* female, two overlapped scales showing the thin membrane. Bars = 5 microns.

conceivable that these scale-like structures are used to transfer some kind of secretion from the abdomen to the wings. This is supported by the oily appearance of the wings. The brushing of wings with abdominal secretion might be used to keep the wings from drying and thus increase the aerodynamic function of the wings, or it might be that some unknown behavioral semiochemical is transferred to the wing.

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ALTITUDINAL PATTERNS IN SPECIES RICHNESS OF NEOTROPICAL TREEHOPPERS (HOMOPTERA: MEMBRACIDAE): THE ROLE OF ANTS

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Abstract.—Treehoppers are sap-feeding insects that vary widely in degrees of both sociality and ant mutualism. Based on these life histories, treehoppers may be classified as (1) species that are ant mutualists and that aggregate as individuals, (2) species exhibiting parental care that are not ant mutualists, and (3) solitary species that rarely interact with ant mutualists. We predicted the availability of ants should influence the distribution of treehopper species that depend upon ants for protection. Because ant abundance has been shown to decline with increasing altitude in tropical regions, we examined the elevational distribution of treehopper species in Colombia that are obligate ant mutualists and those treehopper species that are not. The proportion of treehopper species that are dependent upon ants for defense declined with increasing altitude. Those species having parental care, that do not rely on ants for defense, were more common at higher elevations. Solitary treehoppers, species that only occasionally interact with ants, did not show a changing relationship with altitude. Thus, mutualistic ants are not only important in the evolution of treehopper life histories but also appear to be important in determining the geographic distribution of treehoppers.

Key Words: membracids, mutualism, altitude, Colombia

Sociality in treehoppers (Homoptera: Membracidae) ranges from solitary species to those with highly developed parental care. Additionally, many species rely on ant mutualists for protection from natural enemies (Wood 1984). In return, treehoppers provide ants with a source of carbohydrates, free amino acids and amides, and water in the form of honeydew (Way 1963). Thus, treehopper sociality and ant mutualism may allow alternative defenses against predators (Wood 1982b). For example, aggregations of nymphs and young adults of many species are tended by ants (Wood 1984). In some of these species, parent females also guard eggs and early instars, but their survival is still dependent on the defense provided by ants (Wood 1977, Bristow 1983, Olmstead 1984). The size of treehopper aggregations and the volume of honeydew produced are important factors contributing to the constancy of ant attendance (McEvoy 1979, Fritz 1982, Wood 1982a, Cushman and Whitham 1989).

Other treehopper species also aggregate, but do not interact with ant mutualists. In these presocial species (species with parental care) parent females actively guard eggs and nymphs protecting them from predators (Hinton 1976, 1977, Wood 1976, 1982b, Eberhard 1986). The benefit of aggregation in these species is the effective guarding of offspring by parent females rather than the attraction of ants (Wood 1976).

Alternatively, some treehopper species are solitary throughout their life cycle, are rare, and may incur lower levels of predation simply by virtue of their crypsis. Because a relatively small volume of honeydew is produced by solitary treehoppers, ant-treehopper mutualisms are relatively uncommon in these species (Wood 1984).

Based on their level of sociality and interactions with ant mutualists, treehoppers may be classified as (1) species that are ant mutualists and that form aggregations as individuals, (2) species with parental care that are not ant mutualists, or (3) solitary species that rarely interact with ant mutualists.

In the tropics, ant mutualisms decline with increasing altitude in myrmecophilous animals (Wood 1984) and plants (Bentley 1977a, b, Koptur 1985). This pattern reflects the decline in ant abundance along an increasing elevational gradient (Janzen 1973, Janzen et al. 1976, Bentley 1977a). The cool air temperatures and high soil moisture of tropical montane regions preclude ants from exploiting these habitats (Bentley 1977a). Koptur (1985) and Bentley (1977b) have shown that nectary plants in areas of low ant activity have alternative defenses against herbivores. Thus, the plasticity of the defensive repertoire of these plants (*Inga* and *Bixa*) permits them to grow in areas where ant activity is low. In contrast, the defensive mechanisms of treehoppers are not labile within species. Consequently, treehopper species that rely solely upon ants for defense are relatively undefended in the absence of ants. Furthermore, the increased conspicuousness of individuals in aggregations formed by ant-dependent species elevates their risk of predation compared to species that do not rely upon ants. Non-attended species reduce their risk of predation in other ways. Specifically, aggregations formed by presocial species are protected by parent females while solitary species are cryptic.

Given the effects of altitude on ant abundance and the importance of ants to some treehopper species, we predicted a decline with increasing altitude in the number of tropical treehopper species that depend upon ants for protection. We also predicted that species not dependent on ants for defense should be more common at higher altitudes in the tropics where ants are rare. We used treehoppers to test our predictions because they have a wide geographic distribution and they exhibit diverse life history types (Wood 1982b, 1984). We chose to restrict our study to the treehoppers of Colombia because it has an altitudinal range of 5000 m and membracid taxonomists have made extensive collections there.

Methods

We obtained locality and altitude records for all treehopper species from the literature (Richter 1940, 1941a, b, 1942a, b, c, 1943, 1945, 1955, Strümpel 1972, 1973, Strümpel and Strümpel 1975, 1978) and used gazetteers and relief maps to determine the altitude of those localities for which authors did not provide this information. We divided the altitudinal gradient into 13 classes of 250 m increments, from sea level to 3000 m and above. We found no records of treehoppers collected above 4200 m in Colombia.

One problem inherent in analyzing collection data from published works is the accuracy of locality records. For example, workers may designate the nearest large city as the collection site rather than a more accurate locality. Because we used published data, such errors may exist in our data set.

We followed Metcalf and Wade (1965) for species synonymies and Deitz (1975, 1983, 1985) for classification at the subfamily and tribal levels. We assumed an equal error rate in species identification across taxa relative to life history type. We used Wood's (1976, 1977, 1984) studies of membracids as well as those by Eberhard (1986), Ekkens (1972), Fritz (1982), Haviland (1925), and Hinton (1976, 1977) to determine sociality and ant mutualism for 330 (86%) of the 384 treehopper species recorded from Colombia.

Table 1. The number of treehopper species within each 250 m altitudinal class are given for Colombian treehoppers exhibiting one of three life history types. The number of species for which life history types was not available or could not be inferred is also given (see text for explanation of life history types).

Altitude Range (in Meters)	Midpoint	No. of Ant Dependent Species	No. of Presocial Species (No Ant Mutualism)	No. of Solitary Species	No. of Species with Unknown Life History Types	Total
0–249	125	40	1	21	2	64
250–499	375	61	2	40	3	106
500–749	625	72	1	35	7	115
750–999	875	51	2	25	6	84
1000–1249	1125	32	3	14	6	55
1250–1499	1375	32	6	11	5	54
1500–1749	1625	5	7	8	4	24
1750–1999	1875	17	11	8	7	43
2000–2249	2125	10	3	8	1	22
2250–2499	2375	0	3	4	1	8
2500–2749	2625	3	7	4	9	23
2750–2999	2875	8	22	14	18	62
3000+	3125	1	3	7	4	15
Total Number of Species		156	45	129	54	384

When sociality or ant mutualism information was not available for a particular species, we designated the life history type on the basis of congeners for which these data were available. In the Membracidae, life history patterns are often invariable within tribes, and with few exceptions, are consistent at the generic level (Wood, personal observation). We categorized each species as one of three types (1) species that aggregate as individuals and that are ant mutualists, (2) presocial species that are not ant mutualists, and (3) solitary species. Appendix A is a list of the treehopper genera and includes data on level of sociality and the presence of ant mutualism.

To control for unequal sampling effort throughout Colombia, we evaluated species richness as the proportion of species with a particular life history type relative to all species with known life history types that occur at that elevational class. For example, in our data set 21 solitary species occurred between sea-level and 250 m. Because 62 treehopper species occur in Colombia between 0 and 250 m, solitary species represent 33.87% of the treehopper species in this elevational class. We assumed that although some zones may be less well sampled than others, the proportions of species approximate the relative richness of species with different life history types. Proportional values were arcsine transformed prior to analysis.

We employed polynomial regression models (SAS Institute 1986) to describe the relationship between altitude and the proportion of treehopper species of each life history type. These models are appropriate because there was no reason to assume the relationship between species richness and altitude was linear. This approach also made it possible to describe the form of the relationship. We used sequential (Type I) sums of squares to determine the order of the polynomial regression that was appropriate (Freund et al. 1986). Initially, we used fourth degree polynomials and retained terms significant at $P < .05$ in the models. We examined the Studentized residuals to determine if our data met the assumptions of the models.

Results and Discussion

We were able to assign life history classification to 330 species of treehoppers in our data set. Of these species, 156 (47.27%) were dependent upon ant mutualists, 45 (13.64%) were presocial species that do not interact with ants, and 129 (39.09%) were solitary. The species richness of treehoppers with each of these three life history types across the altitudinal gradient is given in Table 1.

In Colombia, the proportion of treehopper species that depend upon ants for protection declines with increasing altitude (Figure 1a). A linear model best described the relationship ($y = 61.99 - 0.014x^1$, $R^2 = .62$, $P < .01$). Because ants are less common at higher elevations (Janzen 1973, Janzen et al. 1976, Bentley 1977a, b, Koptur 1985), treehoppers in these zones may be at a higher risk of predation than those occurring at lower elevations where ants are more abundant. Thus, our data supported our hypothesis that the altitudinal distribution of treehoppers that depend upon ants for protection reflects the availability of ant mutualists.

We found a significant positive relationship between altitude and the proportion of presocial treehopper species that are not ant mutualists. A linear model best described the relationship (Fig. 1b; $y = 2.71 + 0.135x^1$, $R^2 = .77$, $P < .01$). Because protection of offspring is provided by parent females rather than by ant mutualists, these species are less likely to be restricted to areas where ants are abundant. For this reason, species with parental care are overrepresented at higher elevations where ants, and consequently ant-dependent treehoppers, are rare.

Because ant-treehopper mutualisms are not common but do occur in solitary treehoppers (Wood 1984), these species should not be restricted to areas in which ant mutualists are common. Our data supported this hypothesis since the proportion of solitary species is nearly equal over the elevational gradient (Fig. 1c) and the proportion of solitary treehopper species was not statistically related to elevation in any of the models tested. Solitary species represent on average 36.77 ± 7.23% (arcsine transformed mean ±1 SD) of the membracid species at any elevation.

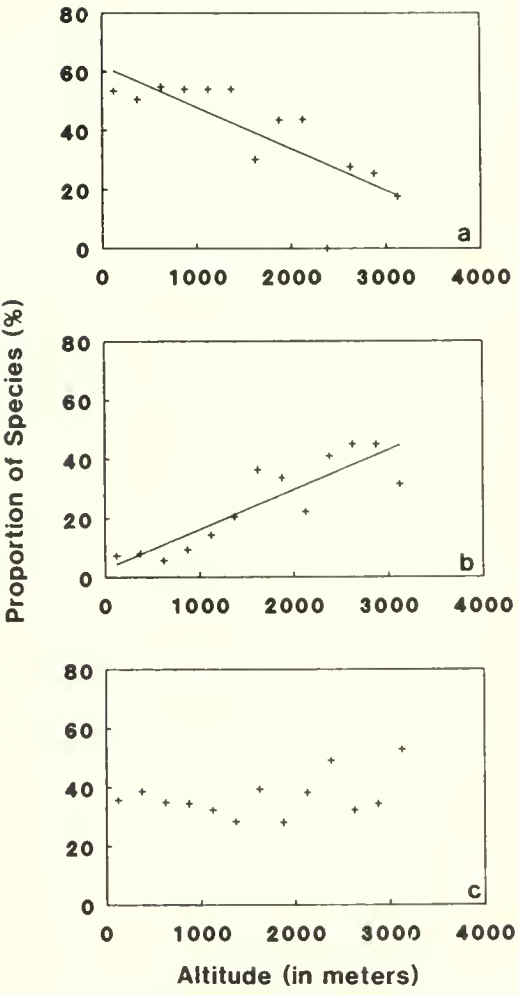

Fig. 1. The relationship between altitude and the proportion of Colombian treehopper species of three life history types: 1a) aggregating ant-dependent species, 1b) presocial species that do not interact with ants, and 1c) solitary species. Proportional values were arcsine transformed. Solid lines represent significant regressions (see text for regression equations and explanation of life history type).

We have focused here upon the relation-

ships between ants, altitude, and treehopper life histories. Admittedly, ant mutualism is not the only selective factor varying across the environmental gradient. Differential plant productivity, seasonality, and a number of other factors may also affect the elevational distribution of phytophagous insects (Begon et al. 1986, Descimon 1986). We assume, however, that the differing selective pressures resulting from the clinal variation in these factors are evenly imposed on species with all three life history types. It appears that the decline with increasing altitude in the relative richness of treehopper species that depend upon ants for protection is due in large part to the corresponding decline in the abundance of mutualistic ants.

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Appendix A. A list of the treehopper genera reported in Colombia including the number of species, life history type, ant mutualism, and references. Life histories were categorized as one of three types: aggregative/ant-dependent, presocial, or solitary.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Subfamily Centrotinae			
Tribe Abelini			
Ischnocentrus	3	Aggregative (8)	Yes (8)
Subfamily Membracinae			
Tribe Aconophorini			
Aconophora	14	Presocial (3, 5, 8)	Yes (8)
Guayaquila	1	Presocial (8)	No (8)
Tribe Hoplophorionini			
Potnia	2	Presocial (8)	No (8)
Ochropepla	2	Presocial (8)	No (8)
Hoplophorion	10	Presocial (8)	No (8)
Alchisme	12	Presocial (8)	No (8)
Umbonia	4	Presocial (1, 5, 6, 8)	No (8)
Tribe Membracini			
Bolbonota	7	Aggregative (1, 8)	Yes (8)
Tritropidia	5	Aggregative (3)	Yes (9)
Erechtia	5	Presocial (8)	Yes (8)
Tylopelta	3	Aggregative (8)	Yes (8)
Leioscyta	14	Aggregative (8)	Yes (8)
Campylenchia	2	Aggregative (8)	Yes (8)
Enchophyllum	6	Aggregative (8)	Yes (8)
Enchenopa	8	Aggregative (8)	Yes (8)
Membracis	28	Aggregative (5, 8)	Yes (8)
Tribe Hypsoprorini			
Notocera	11	Aggregative (8)	Unknown
Philya	4	Solitary (8)	No (8)
Hypsoprora	8	Unknown	Unknown
Sphongophorus	15	Solitary (8)	Unknown
Subfamily Darninae			
Darnoides	4	Unknown	Unknown
Hypheodana	1	Unknown	Unknown
Tribe Cymbomorphini			
Cymbomorpha	1	Solitary (8)	No (8)
Tribe Darnini			
Darnis	3	Solitary (8)	No (8)
Hebetica	2	Unknown	Unknown
Stictopelta	2	Solitary (8)	No (8)
Alcmeone	1	Solitary (8)	No (8)
Tribe Hyphinoini			
Bubalopa	2	Unknown	Unknown
Hyphinoe	2	Solitary (5, 8)	No (8)
Tomogonia	2	Unknown	Unknown
Tribe Hemikypthini			
Proterpia	1	Unknown	Unknown
Atypa	1	Solitary (8)	No (8)
Subfamily Smiliinae			
Tribe Acutalini			
Acutalis	4	Solitary (8)	No (8)

Appendix A. Continued.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Euritea	2	Unknown	Unknown
Thrasymedes	4	Solitary (8)	No (8)
Tribe Micrutalini			
Micrutalis	9	Solitary (8)	Yes (8)
Tribe Ceresini			
Antonae	4	Unknown	Unknown
Centrogonia	4	Solitary (9)	Unknown
Penichrophorus	11	Solitary (9)	Unknown
Ilithucia	2	Unknown	Unknown
Melusinella	1	Unknown	Unknown
Ceresa	9	Solitary (9)	No (9)
Stictolobus	2	Solitary (9)	No (9)
Vestistilus	2	Solitary (8)	No (8)
Cyphonia	8	Solitary (8)	No (8)
Poppea	3	Aggregative (8)	Yes (8)
Tribe Amastrini			
Vanduzea	2	Aggregative (8)	Yes (2, 8)
Harmonides	3	Aggregative (8)	Yes (8)
Tynelia	2	Aggregative (3)	Unknown
Lallemandia	1	Unknown	Unknown
Amastris	7	Solitary (8)	Yes (1, 8)
Tribe Smiliini			
Telamona	1	Solitary (9)	Unknown
Antianthe	3	Presocial (5, 8)	Yes (8)
Tribe Tragopini			
Horiola	2	Presocial (3, 8)	Yes (8)
Tragopa	23	Solitary (8)	Yes (8)
Stilbophora	2	Aggregative (9)	Unknown
Chelyoidea	1	Aggregative (9)	Unknown
Tropidolomia	2	Aggregative (9)	Yes (9)
Tribe Polyglyptini			
Eucatoriana	1	Unknown	Unknown
Heranice	7	Unknown	Unknown
Adippe	2	Presocial (8)	Yes (8)
Dioclophara	2	Unknown	Unknown
Ennya	10	Presocial (8)	No (8)
Hille	4	Presocial (3)	Unknown
Polyglyptodes	2	Presocial (8)	No (8)
Maturnaria	6	Unknown	Unknown
Metheisa	1	Presocial (8)	Yes (8)
Polyrhyssa	1	Unknown	Unknown
Entylia	1	Presocial (5, 7, 8)	Yes (7, 8)
Polyglypta	2	Presocial (1a, 5, 8)	No (8)
Aphetea	3	Presocial (3, 8)	Yes (1, 8)
Phormophora	1	Unknown	Unknown
Subfamily Stegaspidinae			
Tribe Stegaspidini			
Bocydium	5	Solitary (8)	No (8)
Stylocentrus	1	Solitary (8)	No (8)
Oeda	2	Solitary (8)	No (8)
Lycoderes	8	Solitary (8)	No (8)

Appendix A. Continued.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Stegaspis	5	Aggregative (9)	Unknown
Euwalkeria	1	Unknown	Unknown
Subfamily Heteronotinae			
Tribe Heteronotini			
Nassunia	2	Aggregative (8)	Yes (8)
Anchistrotus	2	Aggregative (9)	Unknown
Heteronotus	3	Aggregative (1)	Yes (1, 8)
Smiliorachis	1	Unknown	Unknown
Rhexia	11	Aggregative (9)	Yes
Total Number of Genera = 84		Total Number of Species = 384	

* 1a) Eberhard 1986, 1) Ekkens 1972, 2) Fritz 1982, 3) Haviland 1925, 4) Hinton 1976, 5) Hinton 1977, 6) Wood 1975, 7) Wood 1977, 8) Wood 1984, 9) Wood, personal observation.

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A REVISION OF *ZACREMNOPS* SHARKEY AND WHARTON (HYMENOPTERA: BRACONIDAE: AGATHIDINAE)

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Abstract.—The genus *Zacremnops* Sharkey and Wharton (Hymenoptera: Braconidae: Agathidinae) is revised. Four species are recognized of which two, **Z. ekchuah** and **Z. coatlicue** are new to science. The nominal species *Z. oranensis* de Fernández and *Z. petiolatus* (Szépligeti) are synonymized with *Z. chiriquensis* (Cameron). A diagnostic key to species is presented and phylogenetic relationships among the species are discussed.

Key Words: Hymenoptera, Zacremnops, revision

INTRODUCTION AND HISTORICAL REVIEW

The genus *Zacremnops* was proposed by Sharkey and Wharton (1985) to include two species, *Z. petiolatus* (Szépligeti) and *Z. albitarsus* (Cresson), previously placed in *Megagathis* Kriechbaumer. De Fernández (1987) revised the species of Argentina and Bolivia and described a new species *Z. oranensis*. Studies of additional material since the publication of these works has indicated two new synonyms, two new species and apparently two morphotypes in one previously described species. These findings are presented in this paper.

PHYLOGENY

The relationships of *Zacremnops* within the Agathidinae were discussed by Sharkey and Wharton (1985) and nothing will be added to the argumentation presented there. The phylogenetic relationships among the species of *Zacremnops* are problematical. The species vary in only a few characters and all of these occur in both states in the outgroups, *Cremnops* and *Labagathis*. The sister group of *Zacremnops, Labagathis,* has a color pattern similar to that of *Z. chiriquensis* and *Z. coatlicue*. Indeed, this color pattern is widespread throughout the secondary outgroup, *Cremnops,* and therefore appears to be the plesiomorphic condition within *Zacremnops*. The predominately black coloration, which is very rare in *Zacremnops* and absent in the monotypic sister group, is hypothesized to be a synapomorphy diagnosing *Z. cressoni* and *Z. ekchuah*. Thus the preferred, though weakly supported, hypothesis can be summarized as follows: ((*Z. chiriquensis*) (*Z. coatlicue*) (*Z. cressoni* + *Z. ekchuah*)) or *Z. cressoni* and *Z. ekchuah* are sister species but the phylogenetic placement of the two other species remains uncertain.

TEXT CONVENTIONS

Abbreviations of depositories follow the conventions of Arnett and Samuelson (1986).

AEIC: American Entomological Institute, Gainesville, Florida, U.S.A.

AMNH: American Museum of Natural History, New York, New York, U.S.A.

ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania.
BMNH: British Museum of Natural History, London, England.
CNCI: Canadian National Collection of Insects, Ottawa, Ontario, Canada.
FSCA: Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.
HNHM: Hungarian Natural History Museum, Budapest, Hungary.
IMLA: Fundación e Instituto Miguel Lillo, Tucuman, Argentina.
MCZC: Museum of Comparative Zoology, Cambridge, Massachusetts.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
TAMU: Department of Entomology Insect Collection, Texas A&M University, College Station, Texas.
UGCA: Department of Entomology Collection, University of Georgia, Athens, Georgia.
USNM: United States National Museum of Natural History, Washington, D.C., U.S.A.
ZMHB: Bereich Zoologisches Museum, Berlin, German Democratic Republic.

Taxonomic Treatment

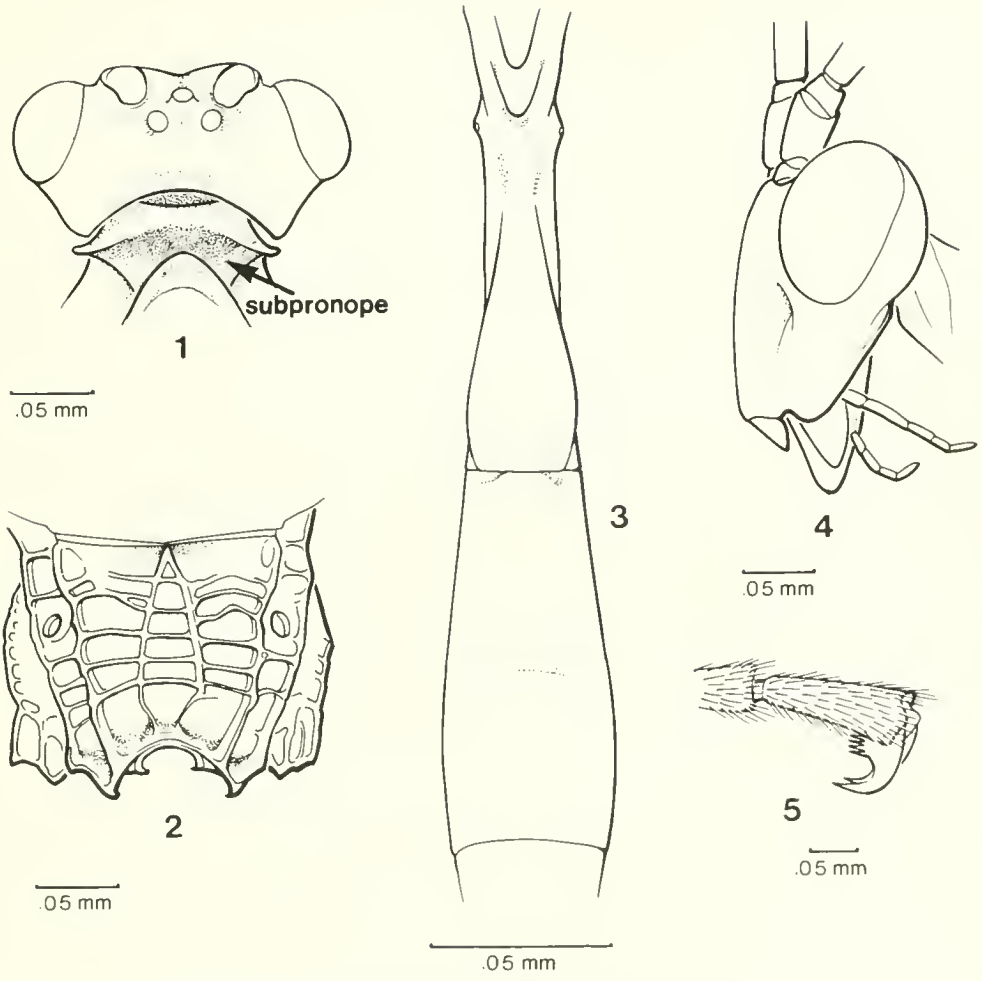
Zacremnops Sharkey and Wharton, 1985.

Type-species.—*Agathis albitarsis* Cresson (= *A. cressoni* Cameron, new name for *albitarsis* Cresson). 1865, p. 63, male, ANSP, type no. 1729.1. Type designation by Sharkey and Wharton (1985).

Description.—Males and females. (From Sharkey and Wharton, 1985). Head (Figs. 1, 4). Distance between median ocellus and lateral ocellus much greater than distance between lateral ocelli; median ocellus situated much lower on face than lateral ocelli; frons, between median ocellus and antennal sockets, smooth and shining, carinae lacking; occiput slightly excavated for reception of pronotum (Fig. 1); malar space long, 0.7–0.8× eye height; longitudinal carina between antennae weak or absent; anterior tentorial pit about 2× closer to eye than to mandibular condyle; maxillary palpus 5-segmented, second and last segments sometimes longest, often all segments subequal (Fig. 4); labial palpus 4-segmented, basal 3 segments subequal, apical segment may be slightly longer (Fig. 4); clypeus almost as high as wide, height : width ratio about 0.8.

Mesosoma (Figs. 1, 2, 5–7).—Anterior and posterior portions of pronotum, medially, separated by deep transverse groove (i.e. subpronopes confluent) (Fig. 1); propleuron without protuberances; sternaulus well developed, usually complete to epicnemial carina (Fig. 7); epicnemial carina approaching pronotum near mid-height of posterior margin of pronotum; at least ventral half of metapleuron areolate-rugose; notauli deeply impressed, smooth; scutellum with posterior transverse ridge weak or absent; propodeum areolate (Fig. 2); propodeal spiracles oval; hind coxal cavities closed; fore tibia lacking spines apically; mid tibia with apical spines but lacking spines admedially; all tarsal claws bifid with pectination basally (Fig. 5); hind trochanterellus lacking longitudinal carina; hind coxa large, about 2× longer than mid coxa; 1RS cell of fore wing quadrate (Fig. 6); 2RS2 vein (really a spurious vein) absent or present as a stub (Fig. 6); cells 1M and 1R1 of fore wing confluent (Fig. 6); last abscissa of Cu vein of hind wing present and well sclerotized basally; last abscissa of Cu vein of hind wing positioned closer to vein A than to vein M+Cu (Fig. 6); 2r-m crossvein (really a spurious vein) of hind wing weakly indicated or completely absent.

Metasoma (Fig. 3).—First tergum long and narrow, 2.6–4.2× longer than apical width; apex of first tergum more than 2× wider than base; all terga mostly smooth; ovipositor longer than metasoma but shorter than body length when fully exposed.



Figs. 1–5. *Zacremnops cressoni* female: 1, dorsal aspect of head and pronotum; 2, propodeum; 3, dorsal aspect three basal metasomal segments; 4, lateral aspect of head; 5, tarsal claw.

Color.—Wings infuscated, with several small hyaline patches (Fig. 6), lacking yellow bands or spots; body mostly to entirely black and usually with some yellow, red or yellowish red color on legs, head, mesosoma or metasoma anteriorly.

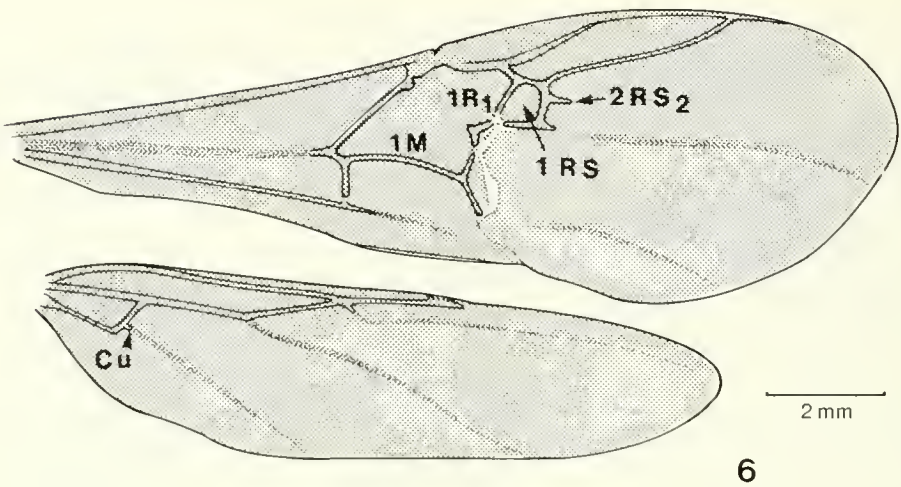
Body length.—Most specimens are large, from 9 to 13 mm; some specimens of *Z. chiriquensis* may be as small as 6.5 mm.

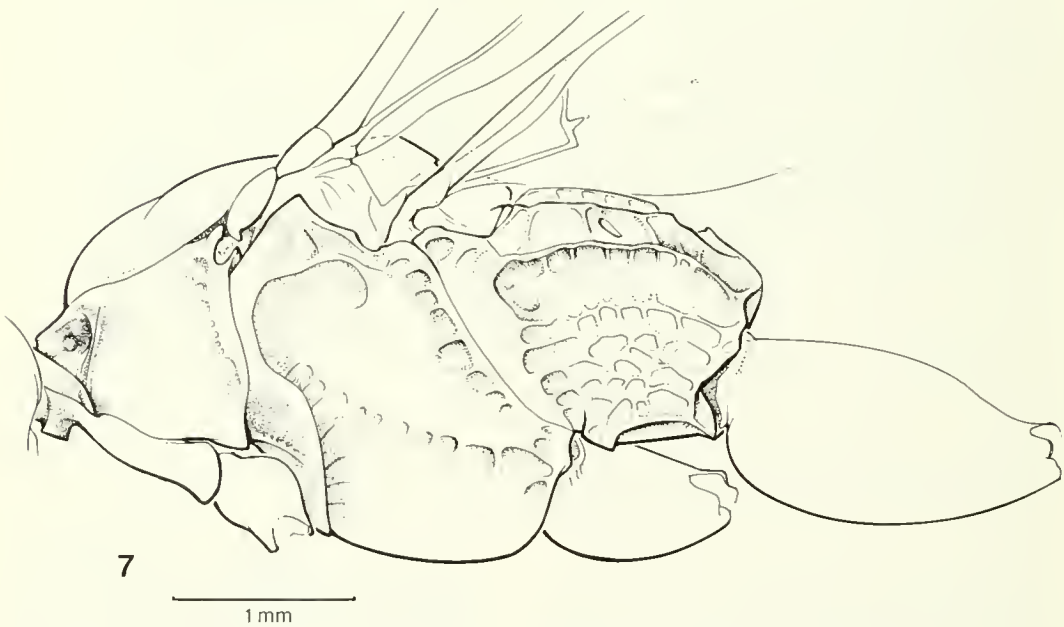
Key to Adults of Species of *Zacremnops*

1. Hind tarsus yellow ..... *Z. cressoni*
1'. Hind tarsus black 2
2(1'). Body entirely melanic ..... *Z. ekchuah*
2'. Body partly reddish orange or yellow 3
3(2'). Mesopleuron black ..... *Z. coatlicue*
Mesopleuron reddish orange ..... *Z. chiriquensis*

Zacremnops chiriquensis (Cameron), New Combination

Agathis chiriquensis Cameron, 1887, p. 399.
Cremnops petiolatus Szépligeti, 1902, p. 65. **Syn. n.**
Megagathis? petiolata (Szépligeti), 1904, p. 122.
Megagathis petiolata: Enderlein, 1920 (1918), p. 167.





Figs. 6–7. *Zacremnops cressoni* female: 6, fore and hind wing; 7, lateral aspect of mesosoma.

Zacremnops petiolatus: Sharkey and Wharton, 1985, p. 603.

Zacremnops oranensis de Fernández, 1987, p. 90. NEW SYNONYMY

Diagnosis.—Males and females. Color mostly black, metapleuron and propodeum reddish orange.

Description.—Antenna with 39–46 flagellomeres; metapleuron rugose reticulate in ventral ⅔, smooth to partly rugose in dorsal ⅓; hind femur from weakly rugose punctate to smooth with scattered punctures; body length 6.5 to 12.5 mm; body color mostly black; mesopleuron, metapleuron and propodeum reddish orange,

some or all of following parts sometimes reddish orange: mouthparts, fore tarsus, base of hind coxa, scutellum, metanotum and basal half of first metasomal segment; rarely mouthparts yellow or reddish orange.

Distribution.—Map 1. Restricted to South America with one record from Panama. Probably widespread north of the 30th parallel except in excessively dry or high areas.

Type material.—*Agathis chiriquensis* (Cameron), Holotype female, PANAMA, David, (BMNH, 3.c.933) (examined). *Zacremnops oranensis* de Fernández, Holotype female. ARGENTINA, Salta, Rio Pescado, Oran, 30.IV.1968, (Porter, IMLA) (examined). *Cremnops petiolatus* Szepligeti, Lectotype female, BRAZIL, Amazonas, Tonantins, (HNHM) (examined).

Depositories.—The more than 400 specimens that I have identified are in the following collections: AEIC, AMNH, BMNH, CNCI, FSCA, HNHM, IMLA, MCZC, USNM, ZMHB.

Remarks.—This species is widespread and rather variable morphologically. De Fernández (1987) based the recognition of a new species, *Z. oranensis,* which I consider to be a junior synonym of *Z. chiriquensis,* on the presence or absence of two longitudinal carinae on the first metasomal tergum. After examining over 400 specimens of this species I have come to the conclusion that the character is variable intraspecifically. The carinae grade from quite strong to completely absent with no correlation with other characters or with geographic distribution. De Fernández (1987) based her conclusions on ten specimens and therefore did not have the advantage of observing the variation of this character. She also used a character to separate *Z. cressoni* from (what I consider to be) *Z. chiriquensis* that does not prove to be valid when many specimens are examined. This is the presence or absence of a complete median longitudinal carina separating the subpronopes.

Z. coatlicue is very close to *Z. chiriquensis* and the two may prove to be conspecific. Though, at present I am persuaded that they are separate species because of three characters: the difference in coloration, with *Z. chiriquensis* having more reddish-orange coloration; the difference in size, *Z. coatlicue* generally being composed of larger specimens; and *Z. coatlicue* having a relatively more robust and wider metapleuron with the dorsal smooth area being substantially larger and mostly lying on a horizontal rather than vertical plane. All of these characters are somewhat variable, but taken together they indicate distinct species.

Zacremnops coatlicue, New Species

Etymology.—Named after Coatlicue, a hideous Mixica chthonic goddess, with a thirst for blood.

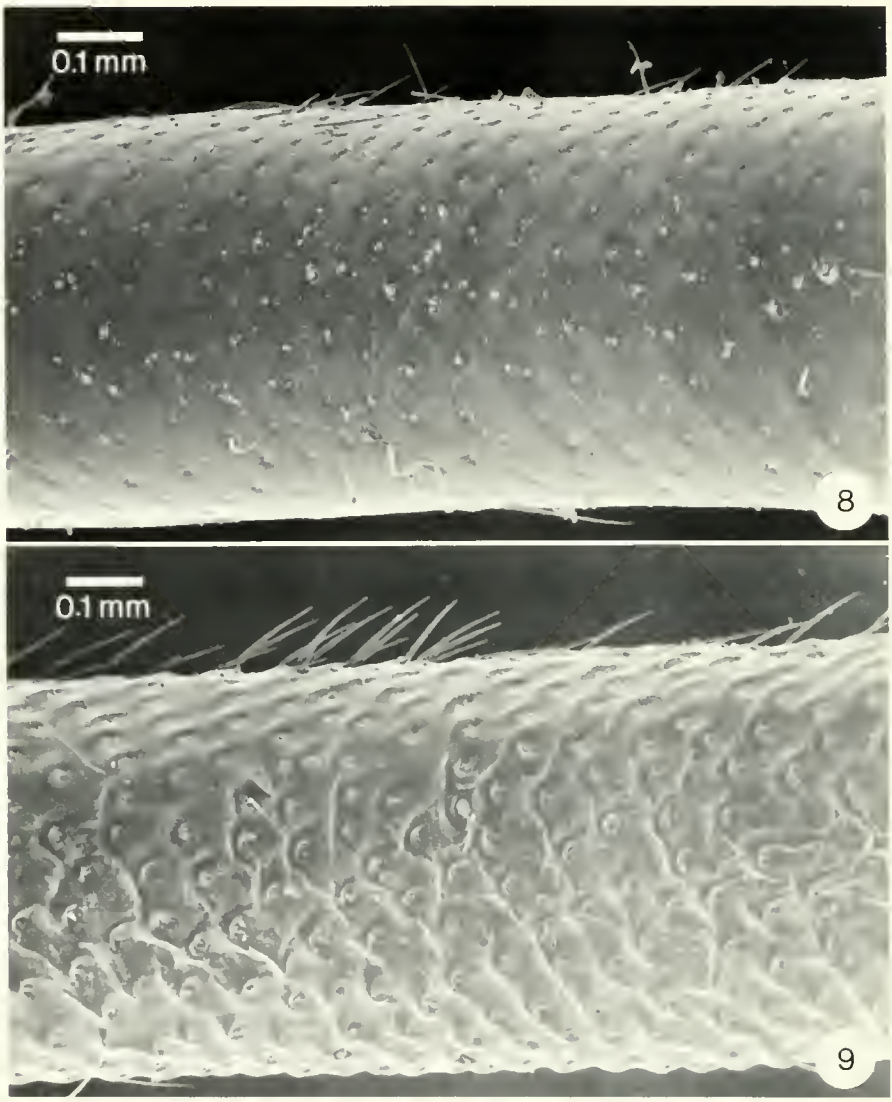
Diagnosis.—Males and females. Color black except metapleuron and propodeum reddish orange.

Description.—Males and females. Antenna with 44–46 flagellomeres; metapleuron rugose reticulate in ventral ⅗, smooth in dorsal ⅖; hind femur from weakly rugose punctate to smooth with scattered punctures ventrally; body length 11.3 to 15.0 mm.; body color entirely black except metapleuron and propodeum reddish orange, rarely (two specimens) the mesopleuron is reddish-black posteriorly.

Distribution.—Map 2. Restricted to Mexican and Central American lowlands. Near the Pacific specimens are found in deciduous forest as far south as Guanacaste Province in Costa Rica and as far North as Sinaloa State in Mexico. Specimens collected near the Caribbean coast are from habitats that once were tropical rainforest, perhaps indicating that the species has a wide range of moisture tolerance.

Type material.—Holotype female, COSTA RICA, Guanacaste, Santa Rosa Park, 22.V.1978 (Janzen, AEIC).

Paratypes.—Allotype, male, same data as holotype except date 8.V.1977. COSTA RICA: Guanacaste: 3 females, same data as holotype except dates 20.V.1978, 21.V.1978



Figs. 8–9. *Zacremnops cressoni* female: 8, ventral aspect of punctate hind femur; 9, ventral aspect of rugose hind femur.

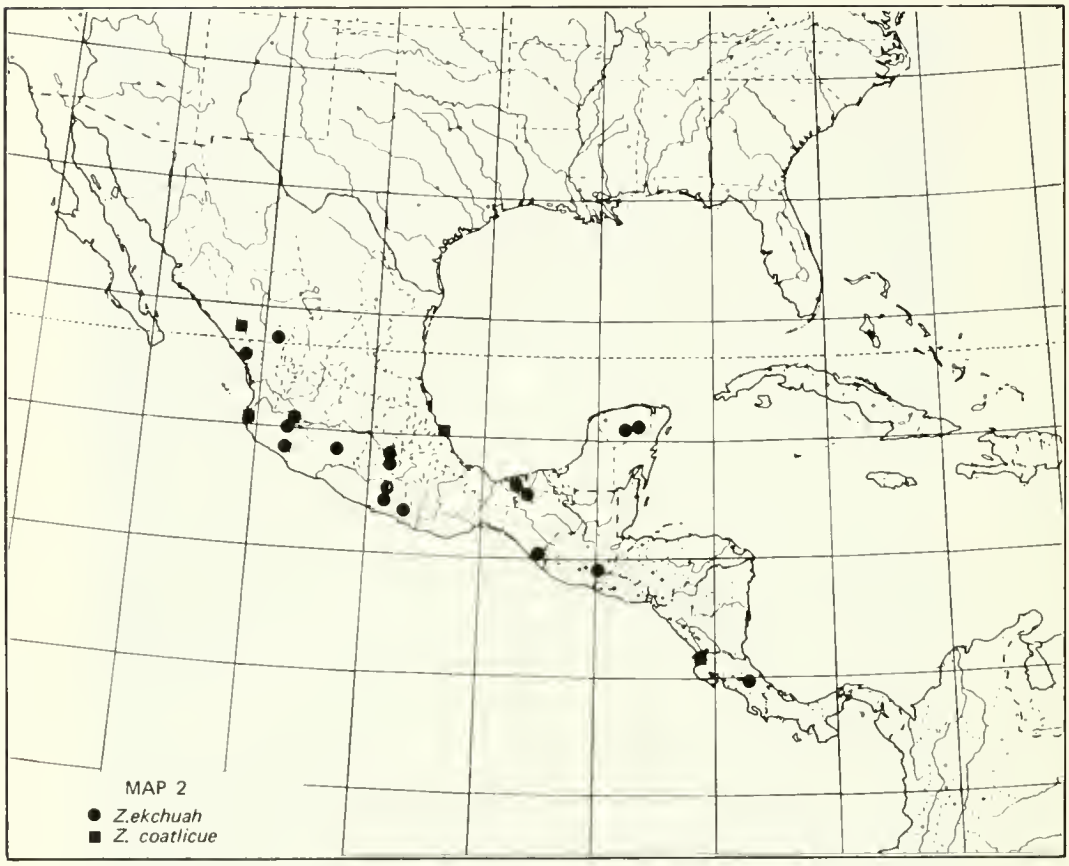
and 18.VI.1978. MEXICO: Jalisco: 1 female, Puerto Vallarta, 18–23.VII.1961 (Grant, CNCI). Sinaloa: 1 female, 8 mi. (13 km) S. Elota, 2.VII.1963, (Parker and Stange, USNM). 1 male, Venodio, (Rosche, USNM). Veracruz: 1 female, Tecolutla, 19.VI.1951 (Evans, AEIC).

***Zacremnops cressoni* (Cameron)**
(Figs. 1–9)

Agathis albitarsus Cresson, 1865, 4: 63. (preoccupied by *A. albitarsus* Spinola, 1840).

Cremnops albitarsis: Schulz, 1906, p. 137.

Map. 1. Distribution of *Z. chiriquensis*.



Map 2. Distribution of *Z. ekchuah* ● and *Z. coatlicue* ■.

Megagathis albitarsis: Enderlein, 1920 (1918), p. 167.

Agathis cressoni Cameron, 1887 (new name for *A. albitarsus*), p. 398.

Cremnops cressoni: Ashmead, 1895 (1894), p. 123.

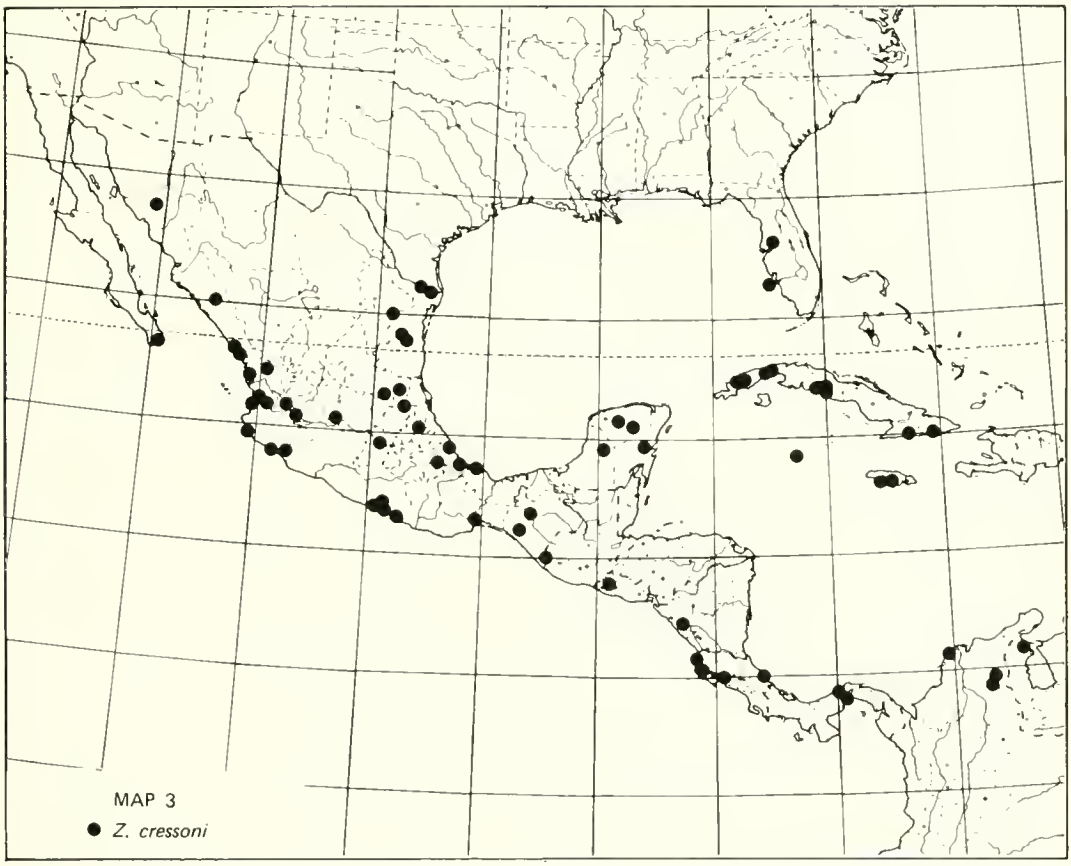
Zacremnops cressoni: Sharkey and Wharton, 1985, p. 599.

Diagnosis.—Males and females. Hind tarsus yellow, remainder of body usually black, often with yellow markings, never with reddish orange markings.

Description.—Males and females. Antenna with 42–49 flagellomeres; metapleuron rugose reticulate in ventral ⅔, smooth to partly rugose in dorsal ⅓; hind femur from rugose to smooth with scattered punctures; body length 9.2 to 13.0 mm; usually body color entirely black except yellow hind tarsus, rarely some or all of following parts also yellow: gena, face, mouthparts, propleuron, mesopleuron, pronotum, mesonotum, fore leg, middle leg, trochanter, trochanterellus, femur and tibia of hind leg, basal ⅓ of metasoma.

Distribution.—Map 3. This is the only species of *Zacremnops* in the U.S.A., occurring in Florida and southern Texas. It is widespread throughout Mexico except in the north-central region, widespread throughout the Greater Antilles, and Central America south to northern Colombia and Venezuela.

Type material.—Holotype male, CUBA, (ANSP) (examined).



Map 3. Distribution of *Z. cressoni*. Specimens with ventral surface of hind femur smooth with punctures ●. Specimens with ventral surface of hind femur rugose to rugose punctate ■.

Depositories.—The 440 specimens that I have identified are in the following collections: AEIC, AMNH, BMNH, CNCI, FSCA, MCZC, MNHN, TAMU, UGCA, USNM.

Remarks.—There appear to be two distinct morphotypes of *Z. cressoni*. Specimens from the Greater Antilles, Florida and the Yucatán peninsula differ from the remainder of the specimens in that the ventral surface of the hind femur is smooth with scattered punctures (Fig. 8) as opposed to rugose (Fig. 9). Members of this population (Greater Antilles etc.) are generally smaller, darker and have fewer flagellar segments. On the basis of these character states, it seems possible that the two populations constitute separate species. Since the known distributions of the two groups are allopatric, I take a conservative approach and treat them as one species.

Zacremnops ekchuah, New Species

Etymology.—Named after Ekchuah, Maya god of merchants, who is said to cover himself in black paint.

Diagnosis.—Males and females. Body entirely black.

Description.—Males and females. Antenna with 45–47 flagellomeres; metapleuron rugose reticulate in ventral ⅔, smooth to completely rugose in dorsal ⅓; hind femur from weakly rugose punctate to smooth with scattered punctures ventrally; body length 10.6 to 15.0 mm; body color entirely black.

Distribution.—Map 2. Found in semitropical and tropical areas from Mexico south to Costa Rica.

Type material.—Holotype, female, MEXICO, Colima, 9 mi. (14.4 km) n.e. Comala, 17–18.VII.1983, (Kovarik, Harrison, Schaffer, CNCI type #20268).

Paratypes.—Allotype, male, same data as holotype. COSTA RICA: 2 males, Turrialba, VIII.1963, (Porter, MCZC). 1 male, Turrialba, 24.V.1944, (Schrader, USNM). GUATEMALA: 1 female, Yepocapa, VIII.1949, (Dalmat, USNM). MEXICO: Chiapas: 20–25 mi. (32–40 km) N. Huixtla, 3000′ (1000 m), 2.VI. and 4.VI.1969, (Teskey and Peterson, CNCI). Durango: 2 males, Nombre de Dios, VIII.1951, (Evans, AEIC). Guerrero: 1 male, 2.1 mi. (3.4 km) N. Cacahuamilpa, 19.VII.1984, (Carroll, Schaffner, Friedlander, TAMU). 4 males, Omiltemi, 8000′ (2700 m), VIII.1904, (Smith, BMNH). 11 females, 4 males, Xucumanatlan, VII.1904, (Smith, BMNH). Jalisco: 1 female, 1 male, Aijijic, 16–18.VII.1966, (Flint and Ortiz, USNM). 1 female, Guadalupe, 26.VII.1951, (Hurd, USNM). 1 male, Puente Grande, 5000′ (1700 m), 20.VIII.1954, (Chillcott, CNCI). Michoacán: 1 male, 18 mi. (29 km) N.W. Quiroga, 6400′ (2100 m), 22.VIII.1962, (Painter and Painter, AEIC), Morelos: 5 females, Cuernavaca, VII–VIII.1944 and 1965, (Krauss, USNM). 1 female, Cuernavaca, IX.1923, (Smyth, USNM). 1 male, 5 mi. (8 km) E. Cuernavaca, 16.VII.1963, (Parker and Stange, USNM). 2 females, Teptoztlán, 20.VIII.1956, (Dreisbach, USNM), 1 female, 3 mi. (4.8 km) S. Tepoztlán, 16.VIII.1962, (Painter and Painter, AEIC). Sinaloa: 2 females, 3 males, Santa Lucia, 4000′ (1300 m), 25.VII–4.VIII.1964, (Mason and McAlpine, CNCI). Tabasco: 1 female, 1 male, Teapa, II–III.1904, (Smith, BMNH). Yucatán: 1 male, Pisté, V.1957, (Townes, AEIC).

Acknowledgments

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A REVISION OF THE NEARCTIC SPECIES OF *DICERURA* KIEFFER (DIPTERA: CECIDOMYIIDAE)

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Abstract.—This revision recognizes 8 species of *Dicerura* in the Nearctic Region including 6 as new. Descriptions are based on the male adults. A key is provided to all species.

Key Words: North America, Palaearctic

Species in the genus *Dicerura* Kieffer are relatively distinctive within the Cecidomyiidae. They are medium sized to relatively large and males can be recognized as members of the genus as alcohol or pinned specimens through examination of their wings, antennal flagellomere numbers and their modified genitalia.

Overall, the Cecidomyiidae are one of the most poorly taxonomically understood groups of Diptera (Vockeroth 1979). This is reflected in the present revision, where only two species of *Dicerura* have been previously named in North America (one in another genus) and an additional 6 species are recognized on the basis of only 14 specimens.

The species in the Palaearctic are better known. Mamaev (1960, 1964, 1966, 1968, 1972, 1975) has described a number of species in the USSR. The species occurring in Latvia, which includes many of those more broadly distributed in the Palaearctic region, have been recently revised by Spungis (1987).

Materials and Methods

This study was based on the examination of 81 males of *Dicerura*, housed in either the CNCI or USNM. Requests for additional material resulted in only negative responses. Cecidomyiidae are not well represented in most North American collections!

The acronyms used to represent the museums from which material was studied are those provided by Arnett and Samuelson (1986):

CNCI—Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, K1A 0C6, Canada.

NYSM—New York State Museum, Biological Survey, 3132 Cultural Education Center, Albany, New York, 12230, USA.

USNM—United States National Entomological Collection, Dept. of Entomology, U.S. National Museum of Natural History, Washington, DC., 20560, USA.

The few specimens studied for this revision were collected either by sweeping, with malaise traps or with a light trap.

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Of the Palaearctic species, I have been able to examine material of only *D. iridis* and *D. rossica*. Otherwise, the Nearctic material described in this paper was compared only to literature descriptions.

Adults were preserved in 70% ethanol and were mounted on microscope slides using a method developed by Leo Forster of our centre. Adults had their wings removed and placed in 15% acetic acid. The head and abdomen were dissected from the thorax and all were placed in 10% KOH which was then heated in a hot water bath. When fully cleared these were placed with the wings in the acetic acid. All parts were then placed through successive baths of 100% 2-propanol, 2-propanol layered over clove oil, pure clove oil, where the antennae and left legs were further separated from the head and thorax respectively, and finally into Canada Balsam on the slide. The antennae and legs were sometimes removed while the specimen was in the Canada Balsam.

Structures were measured using a micrometer in a Nikon compound microscope.

I used the terms provided by Gagné (1981) for discussing various characters.

Type specimens in the Canadian National Collection are given numbers in a reference text and these numbers are reported here with the description of the type locality of each named species as 'CNC No.' Some locality labels are accompanied by a 'CD' number. These refer to detailed notes for a given locality housed in the Diptera Unit of the Biosystematic Research Centre.

Because of a lack of phylogenetic resolution, the species are arranged alphabetically in the text.

Dicerura Kieffer

Dicerura Kieffer 1898: 57. Type-species *Dicerura scirpicola* Kieffer (by monotypy).

Iridomyza Rübsaamen 1899: 67. Type-species *Iridomyza kaltenbachii* Rübsaamen (= *Dicerura iridis* (Kaltenbach)) (by monotypy).

Hormosomyia Felt 1919: 220. Type-species *Hormosomyia oregonensis* Felt (by original designation).

Ulmomyia Mamaev 1960: 1521. Type-species *Ulmomyia rossica* Mamaev (by original designation).

Neosynepidosis Parnell 1971: 313. Type-species *Neosynepidosis furcata* (Felt) (by original designation). NEW SYNONYM.

Diagnosis.—*Males:* only Holarctic Cecidomyiidae with the following combination of character states: 14 antennal flagellomeres; first tarsomere of each leg shorter than second; M_3 present (in some barely discernable); CuA_1 absent; parameres fused; gonostylus lacking tooth or dense apical brush.

Description.—*Male:* coloration: head, thorax, legs, abdomen light to dark brown, thorax with vittae evident; wings pale to generally infuscated.

Head: eye bridge either present or absent (with a gap equal to 2–3 ommatidia); antenna with 14 flagellomeres; flagellomeres with well developed node and neck, each with basal encircling circumfila, with one or two extensions distally; palpus with 4–5 segments.

Thorax: with dorsal outline of scutum and scutellum in lateral view forming an uninterrupted curve; dorsocentral, acrostichal, anepisternal setae present; anepimeral, katepisternal setae present or absent.

Wing: with macrotrichia on membrane and veins; Rs lying in similar direction as R_{4+5}; R_{4+5} extending past apex of wing; apex of M_{1+2} present or absent; apical portion of M_3 present or absent; CuA_1 absent; CuA_2 present.

Legs: first tarsomere of each leg with apical projection; claws with 2–4 ventral teeth; empodium about ⅓–½ length of claw.

Abdomen: posterior setae on tergites arranged in continuous transverse row or in two lateral groups.

Genitalia: tergite 9 densely pruinose; cerci present on hypoproct; parameres fused, forming an aedeagal guide posterodorsally,

Table 1. List of species now placed in the genus *Dicerura*.

adunca n. sp. Borkent. Ontario, Canada.
barbata Mamaev 1966: 226. Ukrainian SSR.
carpiensis n. sp. Borkent. Ontario, Canada.
cooperi n. sp. Borkent. Newfoundland, Canada.
complicata Spungis 1987: 27. Latvia.
curva n. sp. Borkent. Ontario, Canada.
dentata Spungis 1979: 84. Latvia.
elongata n. sp. Borkent. Arizona, USA.
foliicola Mamaev 1968: 614. Maritime Territory, USSR.
fungicola (Mamaev) 1964: 904 (*Ulmomyia*). Moscow Region, USSR.
furcata (Felt) 1907: 52 (*Winnertzia*). New York, USA. NEW COMBINATION.
furculata Mamaev 1968: 614. Ukrainian SSR.
iridis (Kaltenbach) 1874: 717 (*Cecidomyia*). Germany.
kaltenbachi (Rübsaamen) 1899: 67 (*Iridomyza*). Germany.
loba n. sp. Borkent. Ontario, Canada.
mixta Spungis 1987: 24. Latvia.
oregonensis (Felt) 1919: 220 (*Hormosomyia*). Oregon, USA.
padi Mamaev 1975: 60. Maritime Territory, USSR.
rossica (Mamaev) 1960: 1521 (*Ulmomyia*). Voronezh region, USSR.
scirpicola Kieffer 1898: 57. Europe.
scirpi Kieffer 1899: 165 (new name for *scirpicola*).
separata Spungis 1987: 26. Latvia.
stipator Mamaev 1972: 113. Maritime Territory, USSR.
triangularis Mamaev 1966: 227. Ukrainian SSR.
unidentata Spungis 1987: 20. Latvia.
xylophila Mamaev 1966: 227. Ukrainian SSR.

with posterolateral barbs present or absent; aedeagus elongate, single or bifid posteriorly; gonocoxite with mediobasal, pruinose lobe; gonostylus lacking tooth, with or without developed mediobasal lobes.

Distribution and bionomics.—The genus is presently known only from the Holarctic Region. Biological information is available for only some of the Palaearctic species where larvae have been collected from the leaf axils of various plants such as *Scirpus sylvaticus, Iris pseudacorus,* and *Acorus calamus,* from rotting wood, from decaying leaves, or from soil (Mamaev 1973, Spungis 1987).

Taxonomic discussion.—All the species that are presently included in *Dicerura* are listed in Table 1. *D. indica* Grover has been recently transferred to *Cryptoneurus* by Grover (1981).

I consider the genus *Neosynepidosis* as a synonym of *Dicerura* because of the fundamental similarity between the species of the two genera. The characters previously considered to distinguish *Neosynepidosis* are now known within *Dicerura*: the presence of circumfila with distal extensions and the presence of an unforked aedeagus.

The only other genus in the Dicerurini in which males are reported to lack a tooth on the gonostylus is in the monotypic genus *Synepidosis* Mamaev (Mamaev 1964). However, Dr. V. Spungis (pers. comm.) has examined the type of *S. longiventris* Mamaev (from Voronezh Province, USSR) and reports that the gonostylus does in fact bear a small tooth.

Mamaev (1966) reported in a generic diagnosis that some *Dicerura* lack teeth on their tarsal claws. Examination of material and literature descriptions show or report that all *Dicerura* possess at least one tooth on their claws. However, one specimen of *D. oregonensis* had the teeth broken off one midleg claw, indicating that this condition may be an artifact of age or preparation.

Female *Dicerura* have been previously described only from several Palaearctic species (Kieffer 1899, Mamaev 1960, 1964, 1966, 1968, Panelius 1965, Spungis 1987). Although I collected several female *Dicerura* in the Nearctic, I was unable to confidently associate these with males, which appear to be more easily differentiated from one another than are females. I was therefore unable to include descriptions of identified females in this paper. Furthermore, the morphological variation of these and previously described Palaearctic females, in combination with our generally poor understanding of the females of Cecidomyiidae, does not allow for a generic diagnosis of the females at this time. Similarly, the

larvae of some Palaearctic species have been described (Kaltenbach 1874, Mamaev and Krivosheina 1965, Rübsaamen 1899, Spungis 1979, 1987) but they too, for the same reasons as for the females, cannot be diagnosed generically.

Panelius (1965) provided a cladistic analysis of the generic relationships within the Porricondylinae. His major groupings indicated that the subfamily is paraphyletic. No synapomorphy was proposed for *Dicerura* and the monophyly of the genus is therefore uncertain. The only character state which may argue for recognition of this clade is the lack of a tooth on the gonostylus of the male. However, outgroup comparisons within the Lestreminae and Cecidomyiinae indicate that both toothed and bare gonostylii are present. In addition, the bare gonostylus of *Dicerura* is not unique within the Porricondylinae (e.g. present in some Winnertzini, some *Porricondyla*), indicating that the character is susceptible to homoplasy. Consequently, the genus may not be monophyletic. Nevertheless, there is a general similarity of appearance of members of the group and they are presented as a single genus in this paper.

Key

Members of the genus *Dicerura* may be recognized as such in the Holarctic Region using Gagné (1981), with the consideration that *Neosynepidosis* is considered a synonym of *Dicerura* here.

The outline of the gonostylus can be markedly affected by differences in position. Care must be taken, therefore, in comparing specimens to the illustrations provided here.

Key to Adult Males of Nearctic *Dicerura* Species

1. Gonostylus with markedly developed mediobasal lobe (Figs. 3A, B, D, 4C) 2
– Gonostylus with no or only slightly developed mediobasal lobe (Figs. 3C, 4A, B, D) 5
2. Gonostylus with portion distal to mediobasal lobes elongate, apex abruptly bent ventrally (Fig. 3D); parameres lacking posterolateral barbs .. .. *curva* n. sp.
– Gonostylus with portion distal to mediobasal lobes relatively short and apex, at most, somewhat bent medially (Figs. 3A, B, 4C); parameres with posterolateral, stout barbs 3
3. Mediobasal lobe pointed distally (Fig. 3A); aedeagus with a single apex and an associated sclerite; tergite 9 markedly bilobed .. *adunca* n. sp.
– Mediobasal lobe rounded distally (Figs. 3B, 4C); aedeagus biramous apically, lacking associated sclerite; tergite 9 truncated or slightly bilobed ... 4
4. Apex of aedeagus with divergent and separate ends (Fig. 3B); parameres parallel sided posteriorly; flagellomere 3 with stem 0.50–0.67 times length of basal node (Fig. 1B) .... *carpiensis* n. sp.
– Apex of aedeagus with ends closely appressed (Fig. 4C); parameres somewhat bulbous posteriorly; flagellomere 3 with stem 0.94 times length of basal node (Fig. 1G) ..... *loba* n. sp.
5. Aedeagus with single apex (Fig. 4B); paramere lacking posterolateral barbs; flagellomere 3 with stem 0.58–0.86 times length of basal node (Fig. 1F) ..... *furcata* (Felt)
– Aedeagus with biramous apex (Figs. 3C, 4A, D); paramere with posterolateral barbs; flagellomere 3 with stem at least 1.00 times length of basal node (Fig. 1C, E, H) 6
6. Tergite 9 truncated posteriorly (Fig. 4A); aedeagus with ends of biramous apex closely appressed for most of length; gonostylus elongate and of nearly equal diameter; flagellomere 3 with stem 1.06 times length of basal node (Fig. 1E) ..... *elongata* n. sp.
– Tergite 9 rounded or bilobed apically (Fig. 3C, 4D); adeagus with ends of biramous apex divergent and distinctly separated; gonostylus tapering to apex; flagellomere 3 with stem more than 1.41 times length of basal node (Fig. 1C, H) 7
7. Parameres forming rounded lobe posteriorly, with apex with bilobed nipple (Fig. 3C); gonostylus thick, squat for most of its length .... *cooperi* n. sp.
– Parameres forming triangular lobe posteriorly, with apex with single nipple (Fig. 4D); gonostylus evenly tapered posteriorly .... *oregonensis* (Felt)

Dicerura adunca Borkent, New Species

Types.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura

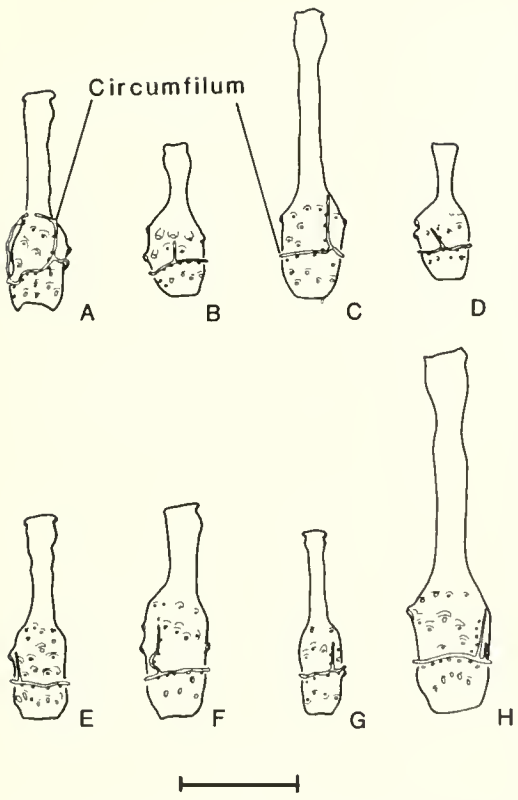

Fig. 1. Third flagellomere of male antenna. Setae and spicules not drawn. Scale = 0.1 mm. A, *D. adunca*. B, *D. carpiensis*. C, *D. cooperi*. D, *D. curva*. E, *D. elongata*. F, *D. furcata*. G. *D. loba*. H, *D. oregonensis*.

adunca Borkent, ♂, Ancaster Spring, Valley, Cons. Area, Wentworth Co., Ont., 6–7-VI-1984, I. M. Smith, CD207, CNC NO. 20343" (CNCI); paratype: 1 male labelled as for holotype (CNCI).

Diagnosis.—*Male:* only Nearctic species in which the circumfilum has two extensions reaching to the distal margin of the flagellomere node; otherwise, this is the only species in which the mediobasal lobe of the gonostylus is short and hooked.

Description of male adult.—*Head:* dorsal eye bridge lacking 1–2 ommatidia medially; antennal length/wing length = 0.90; antennal flagellomere 3 with stem 1.00–1.39 length of basal node (Fig. 1A), circumfilum a basal ring with two extensions reaching to distal margin of node; palpus with 5 segments.

Wing: length = 2.5 mm; M_{1+2} absent, M_3 present apically; halter with moderately elongate stem (Fig. 2A).

Genitalia (Fig. 3A): tergite 9 narrowed posteriorly, bilobed; gonocoxites with slight bilobed posteromedial projection; gonostylus with anteroventral dense patch of short setae, with short, hooked, densely setose mediobasal lobe, gonostylus of similar diameter to rounded apex; paramere forming elongate, somewhat parallel sided projection posteriorly, with very rounded apex, posterolateral margins with double row of short, stout barbs; aedeagus undivided at midlength, with single pointed apex, with subapical barbs, associated oval sclerite.

Taxonomic discussion.—Aside from the characters noted in the diagnosis, this species is unique in the presence of a separate sclerite associated with aedeagus.

Derivation of specific epithet.—The name *adunca* (bent inward) refers to the shape of the mediobasal lobe on the gonostylus.

Dicerura carpiensis Borkent, New Species

Types.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura carpiensis Borkent, ♂, 3 km E. Carp, Ont., 19-V–3-VI-1983, A. Borkent, CD42, Malaise trap, CNC No. 20344" (CNCI); paratypes: 1 male labelled as for holotype; 1 male from km 75–125, Dempster Hwy, Yukon Territory (19-VI-1984, S. & J. Peck) (CNCI); 1 male from Springwater Cons. area, nr. Alymer, Ont. (27-VI-11-VII-1984, K. Ferguson) (CNCI); 1 male from Motts Creek, Atlantic Co., New Jersey (21-V-?, R. J. Gagné).

Diagnosis.—*Male:* only Nearctic species with a gonostylus with an apically rounded mediobasal lobe and with a relatively short stem on the flagellomeres (flagellomere 3 with stem 0.50–0.67 times length of basal node).

Description of male adult.—*Head:* dorsal

eye bridge 3–4 ommatidia wide; antennal length/wing length = 0.64–0.69; antennal flagellomere 3 with stem 0.50–0.67 length of basal node (Fig. 1B), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 2.35–2.81 mm; M_{1+2} absent, M_3 present apically; halter with moderately elongate stem (Fig. 2B).

Genitalia (Fig. 3B): tergite 9 somewhat truncated to rounded posteriorly; gonocoxites with single, posteromedial concavity with small, medial, posteriorly directed lobe, bordered laterally by slightly developed lobes; gonostylus with anteroventral dense patch of short setae, with well developed, densely setose mediobasal lobe, gonostylus distal to mediobasal lobe gradually tapering; paramere forming elongate, somewhat parallel-sided projection posteriorly, with apex bilobed, posterolateral margins with short, stout barbs; aedeagus undivided at midlength, biramous for apical quarter, with ends distinctly separate for their entire length, lacking spicules.

Taxonomic discussion.—All specimens were collected with malaise traps except for the male from the Yukon Territory which was collected with a car net (net mounted on a vehicle).

Derivation of specific epithet.—The name *carpiensis* refers to the type locality, near Carp, Ontario, where the author resided for several years.

Dicerura cooperi Borkent, New Species

Type.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura cooperi Borkent, ♂, CNC No. 20345, 3 km. N. Picadilly, Nfld. [Newfoundland], 25-VI-83, A. Borkent, CD71, Sweeping grass" (CNCI).

Diagnosis.—*Male:* only Nearctic species with parameres forming rounded lobe posteriorly, with its very apex bearing a bilobed nipple and with a thick, squat gonostylus bearing a short mediobasal lobe.

Description of male adult.—*Head:* dorsal eye bridge 2 ommatidia wide; antennal length/wing length unknown (terminal flagellomeres missing); antennal flagellomere 3 with stem 1.76 length of basal node (Fig. 1C), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 2.77 mm; M_{1+2} absent, M_3 present apically; halter with elongate stem (Fig. 2C).

Genitalia (Fig. 3C): tergite 9 slightly bilobed posteriorly; gonocoxites with single, medially convex posteromedial concavity, bordered laterally by slightly developed lobes; gonostylus with anteroventral dense patch of short setae, with short, densely setose mediobasal lobe, gonostylus tapering gradually to apex, small apical projection slightly bent medially; paramere forming wide, somewhat rounded projection posteriorly, very apex with bilobed nipple, posterolateral margins with short, stout barbs; aedeagus undivided at midlength, biramous for apical half with ends distinctly separate and ridged, lacking spicules.

Taxonomic discussion.—*D. cooperi* is somewhat similar to the Palaearctic *D. dentata*. However, *D. dentata* differs in having the apex of the parameres entirely rounded while in *D. cooperi* the parameres have an apical, bilobed nipple. In addition, the aedeagus of *D. dentata* is straight apically but this may be an artifical difference due to position.

Derivation of specific epithet.—The name *cooperi* is given in recognition of Mr. Bruce E. Cooper. A number of specimens he collected were important to this study and reflect his major contributions to the growth, health and welfare of the Diptera collection housed in the Canadian National Collection.

Dicerura curva Borkent, New Species

Types.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura curva Borkent, ♂, Springwater Cons. area, nr. Alymer, Ont., 27-VI–11-VII-1984, K. Ferguson, CD 253, CNC No. 20346"

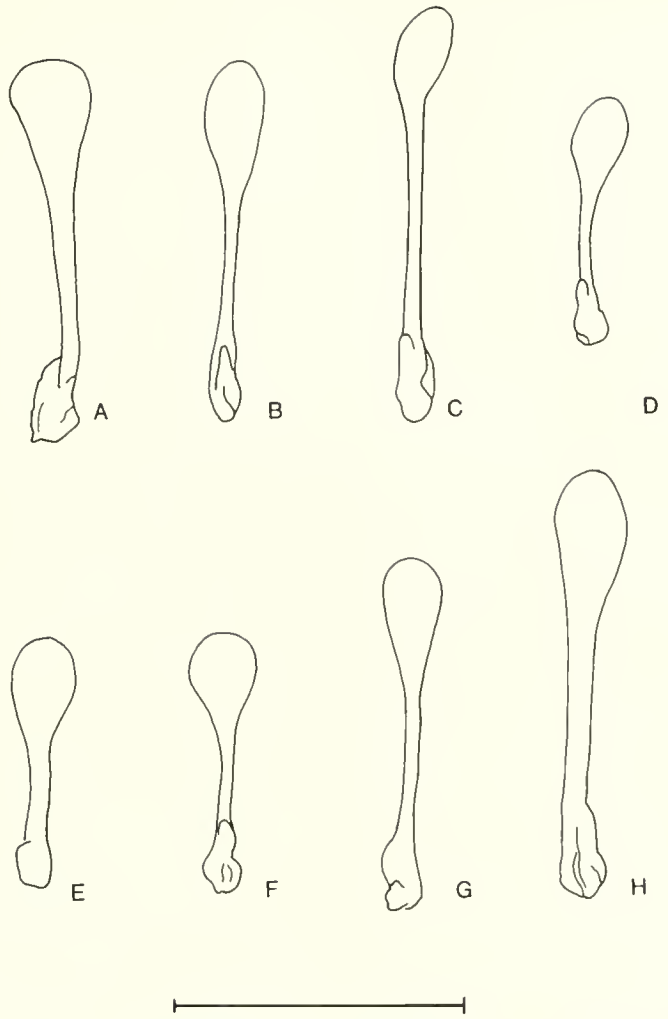

Fig. 2. Outline of male halter. Scale = 0.5 mm A, *D. adunca.* B, *D. carpiensis.* C, *D. cooperi.* D, *D. curva.* E, *D. elongata.* F, *D. furcata.* G, *D. loba.* H, *D. oregonensis.*

(CNCI); paratypes: 1 male from 4 km NW Kagawong, Manitoulin Is., Ontario, 1–16-VI-1982, A. Ritchie (CNCI); 1 male from Cheticamp, Nova Scotia, 6-VI-1984, B. E. Cooper (CNCI).

Diagnosis.—*Male:* only Nearctic species with a gonostylus with a well developed mediobasal lobe and an apex which is bent ventrally.

Description of male adult.—*Head:* dorsal eye bridge 3–6 ommatidia wide; antennal length/wing length = 0.62–0.67; antennal flagellomere 3 with stem 0.76–0.88 length of basal node (Fig. 1D), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 1.9–2.4 mm; M_{1+2} absent, M_3 barely discernable apically; halter with relatively short stem (Fig. 2D).

Genitalia (Fig. 3D): tergite 9 somewhat truncated to rounded posteriorly; gonocoxites with single, posteromedial concavity with small, medial, posteriorly directed lobe, bordered laterally by slightly developed

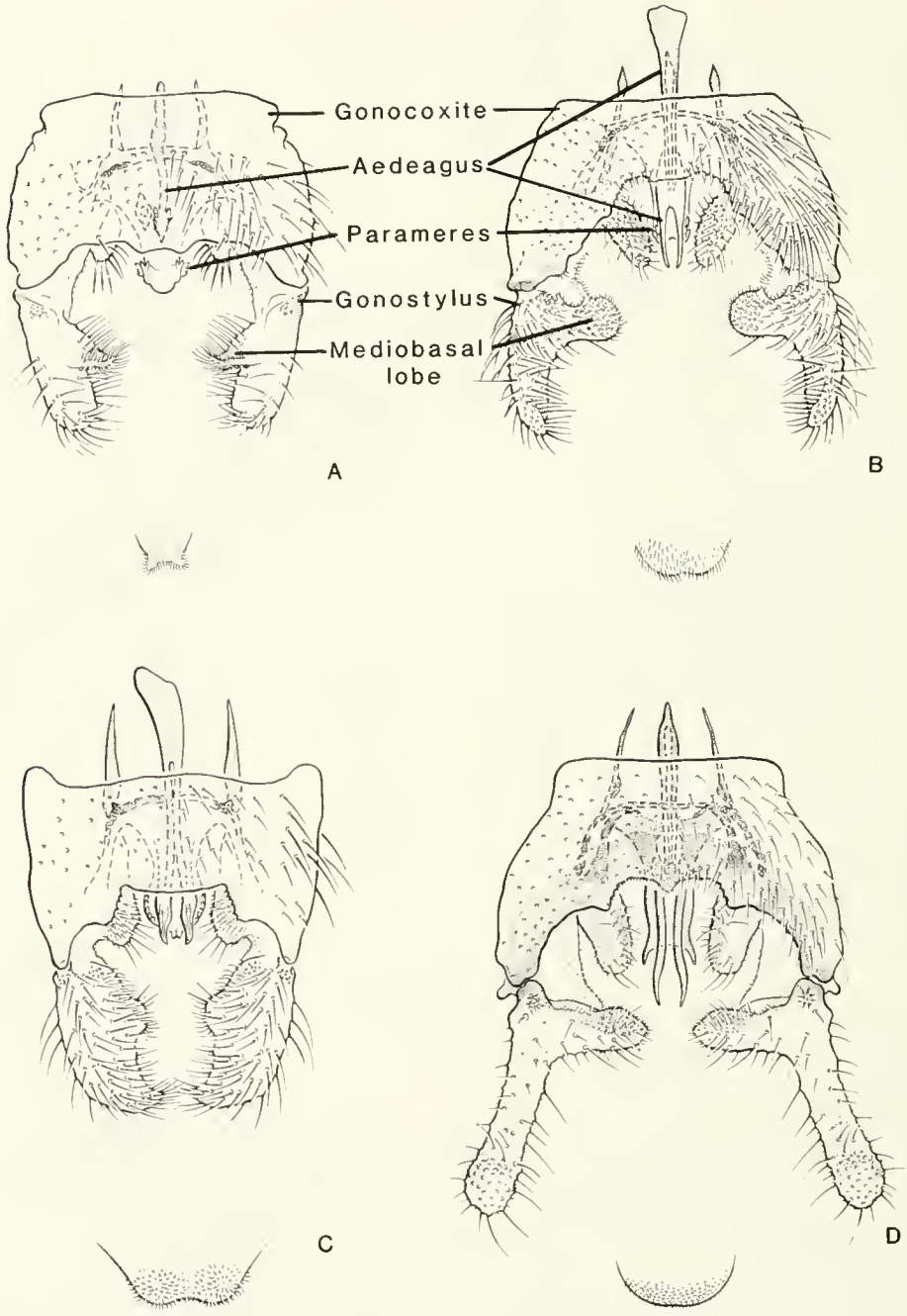

Fig. 3. Male genitalia in ventral view; apex of tergite 9 drawn below. A, *D. adunca*. B, *D. carpiensis*. C, *D. cooperi*. D, *D. curva*.

lobes; gonostylus with anteroventral dense patch of short setae, with well developed, densely setose mediobasal lobe, gonostylus distal to mediobasal lobe of equal diameter, with very apex abruptly directed ventrally; paramere forming elongate, somewhat parallel-sided projection posteriorly, with apex bilobed, posterolateral margins lacking barbs; aedeagus undivided at midlength, biramous for apical half, with ends distinctly separate for their entire length, lacking spicules.

Taxonomic discussion.—This species is very similar to the Palaearctic *D. separata* but tergite 9 is not so tapered apically, the parameres have posteriorly directed barbs apically, and the mediobasal lobe of the gonostylus is proportionally larger. If further collection supports the view that these two are separate species, they are probably sister species, based on the shared unique conformation of the apex of the gonostylus.

The two specimens from Ontario were collected with a Malaise trap.

Derivation of specific epithet.—The name *curva* refers to the unusual subapical curve in the gonostylus of the male of this species (shared by *D. separata* in the Palearctic).

Dicerura elongata Borkent, New Species

Type.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura elongata Borkent, ♂, USNM, Portal, Cochise Co., Ariz., VIII-1-67, at light, Saul and Suzy Frommer, Can. Balsam" (USNM).

Diagnosis.—*Male:* only Nearctic species with a markedly elongate gonostylus, of nearly constant diameter, and lacking a well defined mediobasal lobe.

Description of male adult.—*Head:* dorsal eye bridge 6 ommatidia wide; antennal length/wing length = 0.91; antennal flagellomere 3 with stem 1.06 length of basal node (Fig. 1E), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 2.39 mm; M_{1+2} present apically, M_3 present apically; halter with short stem (Fig. 2E).

Genitalia (Fig. 4A): tergite 9 truncate with posterolateral corner with lobe; gonocoxites with posteromedial concavity with medial spiculose lobe, bordered laterally by fleshy lobes; gonostylus with anteroventral dense patch of short setae, lacking mediobasal lobe (patch of spicules present), gonostylus of nearly constant diameter to rounded apex; paramere forming expanded projection posteriorly, truncated apically, posterolateral margins with short, stout barbs; aedeagu divided at midlength, biramous apically with ends closely appressed, lacking spicules.

Derivation of specific epithet.—The name *elongata* refers to the distinctive, elongate gonostylus of the male of this species.

Dicerura furcata (Felt), New Combination

Winnertzia furcata Felt 1907: 148. Holotype, male adult on microscope slide, not seen (housed in USNM on long term loan from NYSM). Type locality, Nassau, New York.

Asynapta furcata: Felt 1908: 420.

Neosynepidosis furcata: Parnell 1971: 313.

Diagnosis.—*Male:* only Nearctic species with a gonostylus lacking a mediobasal lobe and with the aedeagus undivided.

Description of male adult.—*Head:* dorsal eye bridge 6–8 ommatidia wide; antennal length/wing length = 0.83–0.86; antennal flagellomere 3 with stem 0.58–0.86 length of basal node (Fig. 1F), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 2.6–3.3 mm; M_{1+2} present apically, M_3 present apically; halter with relatively short stem (Fig. 2F).

Genitalia (Fig. 4B): tergite 9 broad, slightly bilobed; gonocoxites with single, evenly curved posteromedial concavity bordered laterally by fleshy lobes, gonostylus with anteromedial dense patch of short setae, lacking mediobasal lobe, gonostylus broadly bent

at midlength; paramere forming parallel sided projection posteriorly, posterolateral margins lacking barbs but forming convoluted thick cuticle; aedeagus divided at midlength, biramous apically with ends closely appressed, lacking spicules.

Taxonomic discussion.—The justification for considering this species, previously placed in *Neosynepidosis*, as a member of *Dicerura* is noted above in the taxonomic discussion of the genus.

Material examined.—I have examined 54 males from the following localities: 14 mi. (22 km) E. Dawson, Y.T.; 40 km. E. Dawson, Y.T.; Kemptville, Ontario; 4 km N. Metcalf, Ontario; 3 km SW Richmond, Ontario; Dunbar Lk., St. Mauricie Provincial Park, Quebec; 19 km N. Grand-Mere, Quebec. Specimens were collected from May 31 to August 22.

Dicerura loba Borkent, New Species

Types.—Holotype, male adult on microscope slide, labelled "Holotype Dicerura loba Borkent, ♂, 3 km E. Carp, Ont., 21-V–11-VI-1984, A. Borkent, CD251, CNC No. 20347" (CNCI); paratype: 1 male labelled as for holotype (CNCI).

Diagnosis.—*Male:* only Nearctic species with the apex of the aedeagus with ends closely appressed, the parameres somewhat bulbous posteriorly and flagellomere 3 with its stem 0.94 times length of the basal node.

Description of male adult.—*Head:* dorsal eye bridge without ommatidia medially; antennal length/wing length = 0.89; antennal flagellomere 3 with stem 0.94 length of basal node (Fig. 1G), circumfilum a basal ring with a single distal extension; palpus with 5 segments.

Wing: length = 2.12–2.55 mm; M_{1+2} barely discernable or absent, M_3 present apically; halter with moderately elongate stem (Fig. 2G).

Genitalia (Fig. 4C): tergite 9 slightly bilobed; gonocoxites with single, evenly curved posteromedial concavity bordered laterally by moderately developed lobes; gonostylus with anteroventral dense patch of short setae, with well developed, densely setose mediobasal lobe, gonostylus tapering gradually to rounded apex; paramere forming wide projection posteriorly, posterolateral margins with short, stout barbs; aedeagus undivided at midlength, thicker for apical third, biramous apically with ends closely appressed for basal portion, distinctly separate at very apex, lacking spicules.

Derivation of specific epithet.—The name *loba* refers to the shape of the mediobasal lobe on the gonostylus of this species.

Dicerura oregonensis (Felt)

Hormosomyia oregonensis Felt 1919: 220. Holotype, male adult on microscope slide, labelled "Type n.g. s.sp. Entomologic Division Hormosomyia oregoniensis (sic) F.R. Cole. 4 Felt. Forest Grove, Ore., C1790, N.Y. State Museum, 13 Mar. 1919" (housed in USNM on long term loan from NYSM).

Dicerura oregonensis: Mamaev 1966: 226; Parnell 1971: 308.

Diagnosis.—*Male:* only Nearctic species with a gonostylus which tapers gradually to its apex, with a poorly defined mediobasal lobe.

Description of male adult.—*Head:* dorsal eye bridge 3–8 ommatidia wide; antennal length/wing length = 1.06–1.14; antennal flagellomere 3 with stem 1.41–1.92 length of basal node (Fig. 1H), circumfilum a basal ring with one or two distal extensions; palpus with 5 segments.

Wing: length = 3.0–5.6 mm; M_{1+2} present apically, M_3 present apically; halter with moderately elongate stem (Fig. 2H).

Genitalia (Fig. 4D): tergite 9 narrowed posteriorly, slightly bilobed; gonocoxites with single, evenly curved posteromedial concavity bordered laterally by moderately developed lobes; gonostylus with anteroventral dense patch of short setae, with short to very short, rounded to angular, in some

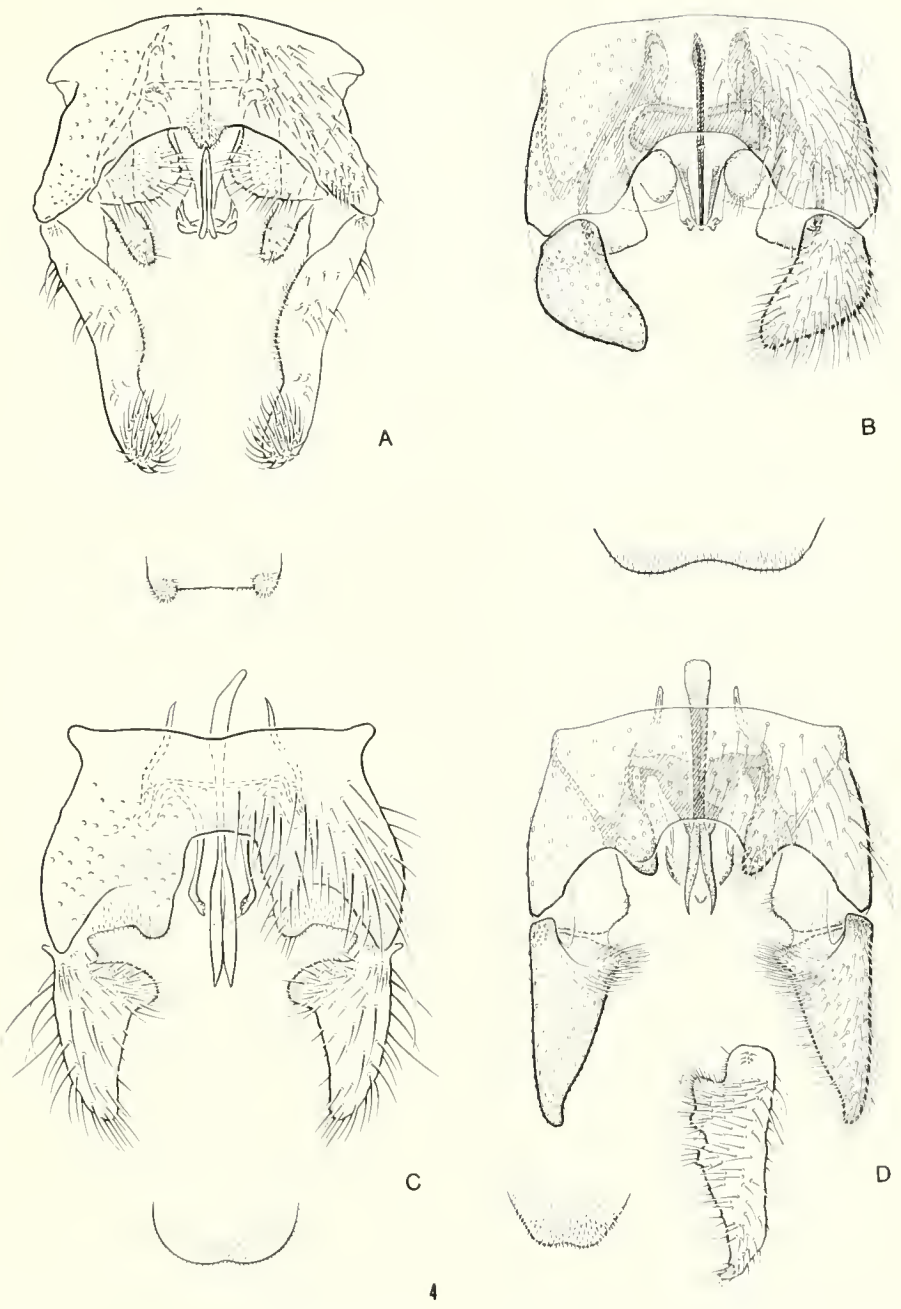

Fig. 4. Male genitalia in ventral view; apex of tergite 9 drawn below. A, *D. elongata*. B, *D. furcata*. C, *D. loba*. D. *D. oregonensis*, with variation in gonostylus shape shown.

poorly defined, densely setose mediobasal lobe, gonostylus tapering gradually to apex, small apical projection slightly bent medially, medial surface of gonostylus smooth to jagged; paramere forming triangular projection posteriorly, posterolateral margins with short, stout barbs, some with subapical margin also with barbs; aedeagus undivided at midlength, biramous apically with ends diverging, a few spicules present or absent.

Taxonomic discussion.—Specimens of *D. oregonensis* were collected by sweeping, with a malaise trap, or at a light.

Of the six specimens examined for this study, some differences were noted in the shape of gonostylus and in the shape and extent of the posterolateral barbs of the parameres. These character states should be restudied once more material becomes available to test the possibility of the presence of more than one species under this name.

The specimen from the Yukon Territory had palpal segments 4 and 5 fused on one side but completely separate on the other.

Although the type label bears a date of March 13, 1919, Felt (1919) reported the date of collection as October 10, 1918. This later date is more consistent with the other specimens of *D. oregonensis* which were collected late in the season.

D. oregonensis is similar to several Palaearctic species. However, I consider the following differences to be significant. In *D. xylophila* the gonostylus is relatively longer, in *D. triangularis* the gonostylus is relatively shorter and broader, in *D. iridis* the ends of the biramous aedeagus are divergent from this base, the spicules on the aedeagus are restricted to the very apex, and the medial area of the gonocoxites is a straight line, and in *D. rossica* the apex of the parameres is rounded.

Material examined.—Five specimens, aside from the holotype, were studied: one specimen from each of Falls Church, Virginia (10-IX-1960, W W. Wirth), km 155, Dempster Highway, Yukon Territory (12-VII-1984, D. M. Wood), 11 km E. Griffith, Ontario (9–20-IX-1984, B. E. Cooper) and 2 specimens from Salmon Arm, British Columbia (29-VIII-1988, A. Borkent).

Derivation of specific epithet.—The name *oregonensis* refers to the state from which the holotype was collected.

Acknowledgments

I thank Mr. Leo Forster for mounting most of the specimens on microscope slides. His typically excellent preparations were crucial to this study.

Mr. Barry Flahey drew most of the male genitalia for this paper and I appreciate his skills in this area. The genitalia of *D. oregonensis* and *D. furcata* were drawn by Mr. Ralph Idema.

Ms. Barbara Bissett provided help with some library work and labelling.

Dr. V. Spungis kindly compared my drawings of Nearctic *Dicerura* to those Palaearctic species in his collection and made comments on their similarities or differences. He also kindly reviewed a manuscript of this revision. I also thank Dr. R. J. Gagné for lending material from the USNM (Washington, D.C.).

Drs. Yves Bousquet and Lubomir Masner made helpful remarks on an early draft of this paper.

Finally I thank Mr. Bruce Cooper (of our Centre) and Mr. Kevin Ferguson (Outdoor Education Center, Alymer, Ontario) for servicing malaise traps which resulted in the capture of some of this material.

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Note

The type locality of *Sciapus pressipes* Parent (Diptera: Dolichopodidae)

Parent (1929, Annls Soc. sci. Brux. (B) 49: 244–246) described *Sciapus pressipes* in his account of the non-European material in the von Roder collection, giving the type locality as "Caroline." He included characters to distinguish the species from other american *Sciapus*, and provided an additional couplet to fit it into Becker's key to the nearctic and neotropical species of the genus (Becker, 1922, Abh. Zool.-Bot. Ges. Wien. 13(1): 361–363). The species has been included in subsequent keys to North American *Sciapus* by Robinson (1964, Misc. Publs Ent. Soc. Am. 4: 112–113) and Steyskal (1966, Proc. Ent. Soc. Wash. 68: 292–294), and was included in the catalog of North American species by Foote et al. (1965, pp. 485–486 in USDA Agr. Hndbk No. 276). However, these subsequent authors all give the distribution as "Carolina," with no extra localities, nor any indication as to whether North or South Carolina is the appropriate state. This suggests that no further material has been collected.

The descriptions of new species in Parent's paper were preceded by a list of localities for both known and previously unknown species (Parent, loc. cit., pp. 169–173). This gives the origin of his material of *S. pressipes* as "Penope (Caroline)." It appears that Penope is an alternative or misspelling of Ponape, and that *S. pressipes* comes from Ponape in the Caroline Is. It is thus a member of the pacific rather than the nearctic fauna. Parent's description shows that whereas *S. pressipes* is unlike any North American species of *Sciapus*, it is very similar to *S. occultus* Parent from the Admiralty Is., particularly in the genitalia and male secondary sexual characters.

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OBITUARY

Anne Marie Wieber
1958–1989

Anne Marie Wieber, an entomologist with the Maryland Department of Agriculture and an officer in the Entomological Society of Washington, died suddenly on May 22, 1989. She perished in a helicopter accident near Cumberland, Maryland, while directing spray operations to control gypsy moths. She resided in Wheaton, Maryland, and is survived by her parents Paul R. and Marilyn J. Wieber of Morgantown, West Virginia, and by a sister, Paula, and a brother, Jerome, both residents of Maryland.

Anne was born in Lakewood, Ohio, where she spent the early years of her life. She lived in Cary, North Carolina, with her family between 1973 and 1975, and periodically returned to North Carolina to visit and vacation along the coast. The family moved to Derwood, Maryland, in 1975, where Anne attended Col. Zadok Magruder High School in Rockville, graduating with the class of 1976. She then entered the University of Maryland where she majored in Entomology, and from which she was awarded the degree of Bachelor of Science in 1980. Anne was employed as an Entomologist by the Forest Pest Management Section of the Maryland Department of Agriculture from 1981 until her death.

Anne became actively involved in the problems of entomological research and pest management while an undergraduate employee of the Department of Entomology, maintaining insect colonies used for research on insect pheromones, and serving as a scout for ornamental and turf pest management programs. As a scout, she refined skills of communicating with the public that made her an invaluable team member in her later career. During the later part of her undergraduate studies, she was a part time employee of the Vegetable Laboratory at the Beltsville Agricultural Research Center (BARC), Beltsville, Maryland (Agricultural Research Service, United States Department of Agriculture). Here she supported research on pests of vegetable crops and commercial mushroom production, preparing illustrations of mushroom flies that were used in scientific presentations.

Upon graduation, Anne became a member of an interagency cooperative team

searching for improved methods to manage the gypsy moth under the technical direction of Ralph E. Webb. Although an employee of the Maryland Department of Agriculture, she was physically located at BARC, initially in association with the Florist and Nursery Crops Laboratory, and later with the Insect Chemical Ecology Laboratory. She participated in a wide variety of projects that involved cooperation with scientists from a number of ARS laboratories and from the USDA-Forest Service, the Animal Plant Health Inspection Service, the University of Maryland, and the Illinois Natural History Survey. Anne cooperated in research to control gypsy moth as a pest of homeowners including evaluation of homeowner spray products for gypsy moth egg mass control, and ground application and systemic implantation of insecticides for control of gypsy moth on individual trees. She collaborated with Michael McManus (USDA-FS, Hamden, Connecticut) to evaluate the use of pheromone traps and burlap banding for gypsy moth monitoring, and was a key participant in a cooperative effort by the Forest Service, Illinois Natural History Survey, and ARS to establish species of gypsy moth adapted microsporidia collected from European gypsy moth populations into North American populations. She led the field research for a detailed study of the hyperparasite complex of the gypsy moth parasite *Cotesia melanoscela* in Maryland. Her last research collaboration involved the design and implementation of a biologically-based gypsy moth suppression program for a county park system. Finally, Anne provided valuable assistance each year to the Maryland Gypsy Moth Cooperative Suppression Program, directing a portion of the spray operations. Reflecting her contributions to the project, Anne coauthored 10 published papers, with another in preparation, and her name will appear on several projected manuscripts. Her collaborators in the *C. melanoscela* study have agreed to publish the results of this research, with Anne to be the senior author.

Anne's interests were not limited to entomology. She had an appreciation for all forms of life and her field work provided great satisfaction for the opportunity to observe nature. She enjoyed pets and over the years had kept tarantulas and ferrets as well as more conventional companions. Anne had as many houseplants as practicality and aesthetics would allow in her home and office. She was especially fond of orchids, succulents and African violets. During the years she worked on Entomology Road in Beltsville, the flower beds around her building were replete with snapdragons, impatiens and marigolds. Anne maintained a small plot of roses for several years at Beltsville that were used in research on rose midges and she also helped with and encouraged many other floricultural projects. She was especially helpful to Floyd F. Smith in his last years, accompanying him to his willow plots and cleaning off his sticky boards.

Anne is missed not only by her colleagues in Entomology, but by her family and multitude of friends. She will be remembered for the enthusiasm and perseverance she displayed in her endeavors, her sense of humor, her love of people. It is a grievous loss that her life and career ended so early.

Acknowledgment.—We wish to thank Maureen Gough for her helpful comments.

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Book Reviews

Insect-Plant Interactions, Vol. I. Edited by E. A. Bernays. CRC Press, Boca Raton, Florida, 1989, 164 pp.

Three years ago an NSF administrator told me that the study of plant-insect interactions—as a viable (and fundable) field ecology—was dead. The central theories had been hashed and rehashed; once innovative experimental approaches were now passé; and controversies that had gripped much of community and population ecology for two decades generated no further debate. An avalanche of data has, in fact, appropriately tamed much of the early enthusiasm for models such as reciprocal coevolution and plant apparency. But to conclude that we have exhausted the subject or—heaven forbid—know all that we need to about the relationships between insect herbivores and their hosts would be scientifically irresponsible. Though they risk obscurity under the guise of an uncommonly common title, the reviews assembled by Elizabeth Bernays in *Insect-Plant Interactions* illustrate the paucity of our knowledge in several areas of this vast subject. The contributors provide a "no-frills" yet thorough treatment of five areas that are rapidly moving into the mainstream of theoretical and empirical plant-insect research.

Bruce Campbell of the Western Regional Research Center, USDA-ARS, begins with a lengthy review (over 570 references) of the importance of intra- and extracellular microbial symbiotes in the nutritional ecology of herbivorous insects. Throughout his discussion he emphasizes how advances in recombinant DNA techniques have replaced primitive manipulations involving antibiotics in studies of microbial symbiotes, particularly endosymbiotes. Molecular techniques have led us beyond the notion that all endosymbiotes are yeasts and toward a more useful understanding of the systematics of symbiotic rickettsiae, bacteria, plasmids, and Bochman bodies. The best evidence suggests that the endosymbiotes supplement nutritionally depauperate host plant resources by synthesizing amino acids, vitamins, and sterols for insect herbivores. Campbell treats extracellular symbiotes with examples from termites, roaches, beetles and flies. In addition to their role in the nutritional adaptation of insects to plants, Campbell also recognizes the potential significance of prokaryotic symbiotes in inducing nongenetic reproductive isolation between different populations of herbivorous insects. Documentation of this phenomenon will have major implications for our understanding of herbivore speciation.

Michael Crawley of Imperial College (U.K.) presents a stimulating synthesis of studies examining the relative impact of vertebrate vs invertebrate herbivores on the population dynamics of plants. First he rather cleverly compares the attributes of vertebrate and invertebrate herbivores, such as body size, metabolic rate, host specificity and mobility because these most influence plant recruitment and mortality. This discussion establishes the hypothesis that vertebrates impose a measurably greater effect on plant communities than do invertebrates. Crawley then tests this hypothesis by examining what is known about the impact of vertebrate and invertebrate herbivores on flower, fruit and seed production, seed and seedling predation, and vegetative growth rate. Finally, he compares observational evidence from herbivore outbreaks, introduced herbivores, and studies of overgrazing, with data generated from experimental manipulations such as fencing exclosures and insecticide applications. Though he presents overwhelming support

for his hypothesis, Crawley concludes by emphasizing that the distinction he draws in this chapter is not between insects and vertebrates, but between small sedentary monophagous herbivores and large mobile polyphagous herbivores. Insects appear to be limited by the abundance of chemically undefended, high quality plants rather than the presence or absence of the plants themselves. Thus, their impact on plant population dynamics and community structure is considered to be ecologically insignificant compared to that of vertebrates.

Chapter 3 is a collaborative effort by J. Riemer (University of Copenhagen) and J. B. Whittaker (University of Lancaster) to draw together a disjunct literature on the effects of air pollutants on insect herbivores and their host plants. This area is truly in its infancy, but Riemer and Whittaker cautiously propose that there is a relationship between aerial pollution and changes in insect attacks on plants. The majority of their evidence comes from European studies which suggest that, on a regional scale, populations of insect predators and parasites generally decline, while herbivore populations—particularly those of sap feeders not directly exposed to the pollutants themselves—increase. The principal hypothesis examined in this chapter is that pollution increases plant susceptibility to herbivore attack by weakening defense systems and/or improving resources in sap or foliage in terms of insect nutrition. The authors freely discuss inadequacies in the existing pool of data and call for controlled manipulations in future studies of this obviously important but heretofore neglected area.

The fourth contribution takes a long overdue look at the extrinsic factors regulating the production of secondary metabolites in plants. This chapter alone makes the volume a worthwhile purchase, for in it Peter Waterman (University of Strathclyde, Scotland) and Simon Mole (Purdue University) critically examine the essence of nearly all plant-insect interactions: the functions and regulation of secondary metabolites. They begin by dismissing the simplistic views of secondary metabolites that dominated plant-insect theory in the 60's and 70's. It is not the 'apparency' of plants that determines the qualitative and quantitative presence of secondary metabolites in plant tissues, but rather a fundamental shift from metabolic products of the shikimic acid pathway (commonly employed by woody perennials) to products derived from acetate or mevalonate (typical of more advanced herbaceous plants). Beyond these phylogenetic restrictions, the authors stress the importance of light intensity and soil nutrient quality in controlling the production and distribution of plant metabolites. Although it is brief, I applaud their discussion of costs related to the production and maintenance of secondary metabolites. Here they make the necessary distinction between energy costs and the cost of substrate depletion, a distinction that has escaped too many ecologists in the past. Of over-riding importance is the chapter's message that insect herbivores are only one of many extrinsic factors influencing the production of secondary metabolites in plants. Evolutionary interactions between plants and insects must be interpreted with this in mind.

Stephen Welter of the University of California concludes the volume with a discussion of the consequences of herbivory on gas exchange and thus the physiological processes of photosynthesis and respiration. His approach is to focus on the impact of various types of herbivory, including that inflicted by defoliators, mesophyll feeders, gall formers, epidermal feeders, phloem feeders, stem borers, and insects attacking roots. The strength of his chapter lies in its portrayal of our current knowledge of the subject, wanting as it is, rather than with patterns or predictions emerging from the data. The effect of herbivores on gas exchange in plants is yet another area about which we know too little to draw reliable conclusions.

I recommend this first volume of *Insect-*

Plant Interactions to anyone wanting to stay abreast of current research trends in this area of ecology, and I commend the editor for her insight in compiling 5 reviews which should convincingly demonstrate to nonbelievers that the science of plant-insect interactions is alive and well.

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Book Review

A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha. By P. Ferrar. 1987. Entomograph, Volume 8. E. J. Brill/Scandinavian Science Press, Leiden, Copenhagen. Two parts (not available separately). 907 pp. $180.00. Hard cover. ISBN 90 04 08539 4.

This century, 90% of which has already passed, has seen enormous progress in the science of Dipterology. The monumental series "Die Fliegen der Palaerktischen Region," almost as old as the century and now nearly completed, has set an example for a similar, Nearctic series that has recently been started. Catalogs for all the major zoogeographical regions have either been published recently or are nearing completion, and several teams of workers have launched a compilation of world catalogs for families. The recently completed "Manual of Nearctic Diptera" has set excellent guidelines for faunal treatments elsewhere, and there are countless smaller contributions. However, all these major contributions, plus the overwhelming majority of smaller publications on Diptera, are based on, or deal entirely with adult flies, whereas the immature stages have received relatively little attention. One exception is Hennig's (1948–1952) series of three books that summarized all descriptive work on immature Diptera available up to the middle of this century. The main reason for this bias stems from the difficulty inherent in locating, collecting, rearing and identifying immature dipterans. This is also the reason that most of the work published on immatures is descriptive and the entire knowledge on these stages is still very fragmentary. Ferrar's guide, in a way comparable to Hennig's books, is a very successful attempt at summarizing the progress made during the second half of the century on a large subgroup of Diptera, the Cyclorrhapha.

Ferrar's monograph is rather conveniently divided into two volumes: a) The text which covers 478 pages in addition to 8 text-figures and numerous tables, which are numbered separately in each chapter; and b) the figures that cover 431 pages including 11 pages presenting a list of the sources. The text is arranged in a simple and efficient way. After the sections entitled "Preface and Acknowledgments" and "Abbreviations" (five of the six abbreviations refer to the five stadia of immature stages, and the sixth—ANIC—to the Australian National Insect Collection), there is a short section (Chapter 1) devoted to techniques and dealing with the preparation and examination of eggs, larvae, and puparia. Chapter 2 is a comprehensive treatment of anatomical features of all immature stadia, and chapter 3 analyzes, mostly in table form, the topic of breeding and other habits of Diptera Cy-

clorrhapha. Chapter 4 is a key to 3rd instar larvae of 74 families, out of the 87 treated in the work. The treatment of individual families, which are presented alphabetically, begins on page 60. The following information is given for each family: 1. Scope and distribution; 2. Economic importance—often treated under the subtitles "Harmful" and "Beneficial"; 3. Notes on literature; 4. Biology—arranged according to the unique biological and ecological features of the family; 5. Immature stages—description of all known stages. Literature is sometimes given under generic or specific titles in the Biology section. The text length for a family ranges from a few lines to more than 15 pages (e.g. Muscidae—22, Drosophilidae—19), with an average of just under 4 pages.

The second volume, with some 5000 figures, is probably the largest assemblage of figures ever published for the Cyclorrhapha as a whole, as well as for many of the included families. The first 1142 figures are a selection of duplications from the rest of the figures, and are arranged in the following general order: egg; first instar larva: whole body, head skeleton, spiracles; second and third instar larvae (same internal order as in first instar); and pupa. The remaining figures are arranged by family, and then again by stage and body part.

Ferrar's guide is, in my opinion, one of the major contributions to Dipterology this century. However, there are several shortcomings and errors, that should be noted. Beginning with the more general ones: Although this work is basically a compilation ("A new summary" in Ferrar's own words) based on over 2000 papers, the author does not explain the procedures used. As a result, there is no feasible way of knowing the extent of the literature review, or which papers were not included. Indeed, many references have been omitted, either unintentionally or deliberately. This deficiency would make it very difficult to trace published descriptions of immatures that are not mentioned in this work. A second point is the lack of indication regarding the author's criteria for either re-writing information, or presenting it unmodified. Likewise, there is no indication as to how many of the described immatures the author has seen or studied himself.

In a compilation of such magnitude it is difficult to correct mistakes of other researchers, or even to resolve inconsistencies or contradictions between different sets of data. It is therefore especially important not to create new confusion. One such inconsistency is on page 29 where the author states that "*Myopites* (Tephritidae) is unique among known Cyclorrhapha in having only 2 slits per spiracular plate in the 3rd instar," but on page 26 (Table 2.3) he says that some Phoridae have 2 "slits" and that Nycteribiidae (page 26) and Streblidae (page 27) have 2 "apertures." Likewise, there is a discrepancy between the statements on pages 12 and 45 with regards to families for which immature stages are not known. The family Asteiidae is included in the list on page 45 only. Later, however, the egg and puparium of *Asteia sabroskyi* are redescribed (page 79). Additional examples of copied errors are given below when dealing with the chapter on Tephritidae. Perhaps due to his Australian background, Ferrar refers repeatedly and with partiality to the Australian fauna. He explains in the preface that because of the alphabetical layout of the families, an index would be largely superfluous. I, however, believe that an index to names, and especially to terminology, would have been desirable. The positioning of the titles of the tables below rather than above the tables is especially disturbing in tables covering more than one page, where the reader sometimes needs to turn the page in order to read the title.

I have tested the key on examples from several well-studied families as well as from poorly known ones, including the undescribed larvae of a species of Canacidae and those of Tethinidae. All except the Tethini-

dae ran smoothly into their families. The Tethinidae dead-ended, which is gratifying for a key that does not include this family (larvae of this family have apparently never been described).

In the second volume it is admittedly convenient to have the separate batch of initial 1142 figures at hand, so that a selection of figures from across the Cyclorrhapha can be viewed easily. However, I believe it would be more practical to omit this luxury of 80 duplicate pages in favor of a proportionate reduction in the price the book, which is very high. The list of figure sources on page 897 does give the relevant references. However, is this a legal substitute for copyrights and receiving permission to copy figures? My final comment about the figures in volume 2 is with regards to their quality. The mixed styles of the figures is less than aesthetic, but is understandable and acceptable. The great majority of the figures are reasonable reproductions, and some of them are, surprisingly, better than the originals. However, the quality of certain figures is extremely low, even to the point of being useless (the figures on page 705 and figure 88.31 are just a few examples).

More specific comments: "Techniques" (Chapter 1). This chapter is generally instructive. The author, however, refers only very briefly to the use of scanning electron microscopy (SEM) for larvae. Although this is a relatively new approach, it is gaining momentum quickly and deserves more than the 10 short lines given to it in this work. It is perhaps appropriate to add here a quick method for studying larvae that I have found satisfactory in most cases: use (with caution) hot 10% KOH to macerate the larva, clean in water, and mount in a drop of glycerin.

I have not taken special efforts to discover errors, but the one on p. 22, where Figure 6.252 was cited was prominent. Such a figure does not exist, and the author probably meant to say Figure 14.6.

Two good practices, on the other hand, deserve mentioning: In volume one the author is consistent in giving in parentheses the family to which every mentioned species belongs. In volume 2 the figure legends are located immediately below their respective figures. These two practices, which are not very common elsewhere, facilitate the use of the work.

In relating to the individual chapters dealing with the various families, I prefer to restrict myself to the chapter dealing with Tephritidae, a family which I myself have been studying for some time. I have only a few comments: The examples of beneficial species are enlightening, but I would also have added a further example, namely the genus *Urophora*, which has been the focus of extensive research in recent years. Several species of this genus have been introduced from Europe to North America, some successfully, to combat knapweed and related weeds there.

The first paragraph of column 2 on page 388 deals with the generalization that all Aciurinae whose hosts are known breed in plants of the families Labiatae, Acanthaceae or Verbenaceae [within Tephritidae this association is practically unique (A.F.)]. Although I am still a strong supporter of this statement, this particular paragraph is erroneous and misleading, partly due to my own earlier mistake. The genus I meant to record in 1979 is *Perirhithrum*, not *Trirhithromyia*. *Perirhithrum* was recently transferred from the Schistopterinae to the Tephritinae but, as this genus is now considered to be in the Aciurinae (Freidberg, unpublished), it supports the generalization about hosts of this group rather than being an exception. Likewise, *Aciurina* is a tephritine (and not an aciurine as might be alluded from its name) and therefore is not an exception to the above generalization, despite the fact that its hosts are Compositae. The only known exception to the above generalization is *Eutreta xanthochaeta* (Tephritinae), a species that induces the formation of stem galls on *Lantana camara* (Verbenaceae).

The only described immatures of a true *Chetostoma* are those of *C. continuans* which are frugivorous on *Lonicera* spp. (Caprifoliaceae; Kandybina, 1966: 679). *Chetostoma completum* (p. 390) is actually a *Chaetostomella* (based on my unpublished observations on specimens from the type series), a genus attacking various Compositae. Finally, some names were misspelled: The correct spelling is *Carpomya* and not *Carpomyia* (p. 389); and *heracleii* (a species of *Euleia*) and not *heraclei* (p. 390). Despite these shortcomings, this chapter makes interesting reading and is an important reference in the study of Tephritidae. I am sure that other researchers will reach the same conclusion with regards to the chapters that deal with families of their own particular interest.

In summary, this excellent work is a must for any laboratory studying Diptera or immatures and ecology of insects. Its appearance is warmly welcomed. As a result of its presence, the necessity for similar sets for the rest of the Diptera became much more prominent.

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BIOLOGY AND MORPHOLOGY OF THE BANANA MOTH, *OPOGONA SACCHARI* (BOJER), AND ITS INTRODUCTION INTO FLORIDA (LEPIDOPTERA: TINEIDAE)

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Abstract.—The general distribution and recent introduction into Florida of the banana moth, *Opogona sacchari* (Bojer) is reviewed. Currently, the principal damage caused by this species in Florida consists of larval stem boring in certain nursery stock and ornamental palms in particular. The biology of the species is summarized and all stages of the insect are described, supplemented by numerous illustrations.

Key Words: Lepidoptera, Tineidae, *Opogona sacchari,* banana moth, moth biology, immature stages

The banana moth, *Opogona sacchari* (Bojer), is known from several tropical-subtropical humid regions around the world but has yet to be reported from the Indo-Australian region. Originally reported from the Mascarene Islands in the Indian Ocean (Bojer 1856, Walker 1863, Butler 1876), the species was later discovered in Africa (Vari and Kroon 1986) as well as islands near the African continent (Walker 1875, Durrant 1925) and Europe (Ciampolini 1973, D'Aguilar and Martinez 1982, Mourikis and Vassilaina-Alexopoulon 1983). More recently the species has spread to South America (Cintra 1975, Giannoti et al. 1977) and the West Indies (Alam 1984). The earliest evidence we have of this species in the New World is represented by adult specimens in the Smithsonian Institution (USNM) that were collected in 1970 from Aragua, Venezuela on potato.

Specimens received for identification from B. Kumashiro of the Hawaiian Department of Agriculture just prior to publication indicate that *O. sacchari* is now established in Hawaii. The species has been reared from rotting coconut tree tops (central whorl of leaves) from Kaneohe, Oahu and from an unidentified palm at Kohala, Hawaii.

Within the last few years *O. sacchari* has become established on various nursery stock in southern Florida, particularly in Dade and Palm Beach Counties (Heppner, Peña, and Glenn 1987). Nursery stock particularly affected in Florida include corn plant or casse (*Dracena fragrans* (L.) Ker-Gaus, variety *massangeana*) and bamboo palms (*Chamaedorea* sp.) as well as Hawaiian good luck plant (*Cordyline terminalis* (L.) Kunth) and aralias (*Polyscias* sp.). Although sugar cane is a major host, *O. sacchari* has not yet been reported on that plant in the United States.

The appearance of this new pest in the United States has necessitated a careful examination of all developmental stages and a report of its biology pertinent to its current significance as a pest of nursery stock in Florida.

Opogona sacchari (Bojer)

Ahucita sacchari Bojer 1856: 21, pl. 5, figs. 1–10.

Opogona sacchari (Bojer).—Vinson, 1938: 56 (synonym of *Opogona subcervinella*).—Viette, 1957: 145; 1958: 4.—Ciampolini, 1973: 221.—Cintra, 1975: 223.—Giannoti et al., 1977: 209.—Declercq and Van Luchene, 1977: 499.—Zimmerman, 1978: 386.—Cintra et al., 1978: 3.—Pigatii, 1978: 21.—Pigatii et al., 1979: 61.—Veenenbos, 1981: 235.—D'Aguilar and Martinez, 1982: 28.—Rotundo and Tremlay, 1982: 123.—Suplicy and Sampaio, 1982: 174.—Bennett and Alam, 1985: 41.—Heppner et al., 1987: 1.

Tinea subcervinella Walker, 1863: 477.

Opogona subcervinella (Walker).—Walsingham, 1907: 713; 1919: 259.—Meyrick, 1930: 321.—Vinson, 1938: 56.—Viette, 1951: 339; 1957: 145 (synonym of *Opogona sacchari*); 1958: 4.—Paulian and Viette, 1955: 147.—Box, 1953: 34.—Davis, 1978: 14; 1984: 22.—Vari and Kroon, 1986: 84, 156.

Hieroxestis subcervinella (Walker).—Meyrick, 1910: 375; 1911: 298.—Cockerell, 1923: 247.—Meyrick, 1924: 556.—Durrant, 1925: 12.—Oldham, 1928: 147.—Rebel, 1939: 63; 1949: 56.—Jannone, 1966: 24.

Gelechia sanctaehelenae Walker, 1875: 192.—Durrant, 1925: 12 (synonym of *Hieroxestis subcervinella*).

Euplocamus sanctaehelenae (Walker).—Wollaston, 1879: 417.

Hieroxestis sanctaehelenae (Walker).—Durrant, 1923: xvii.

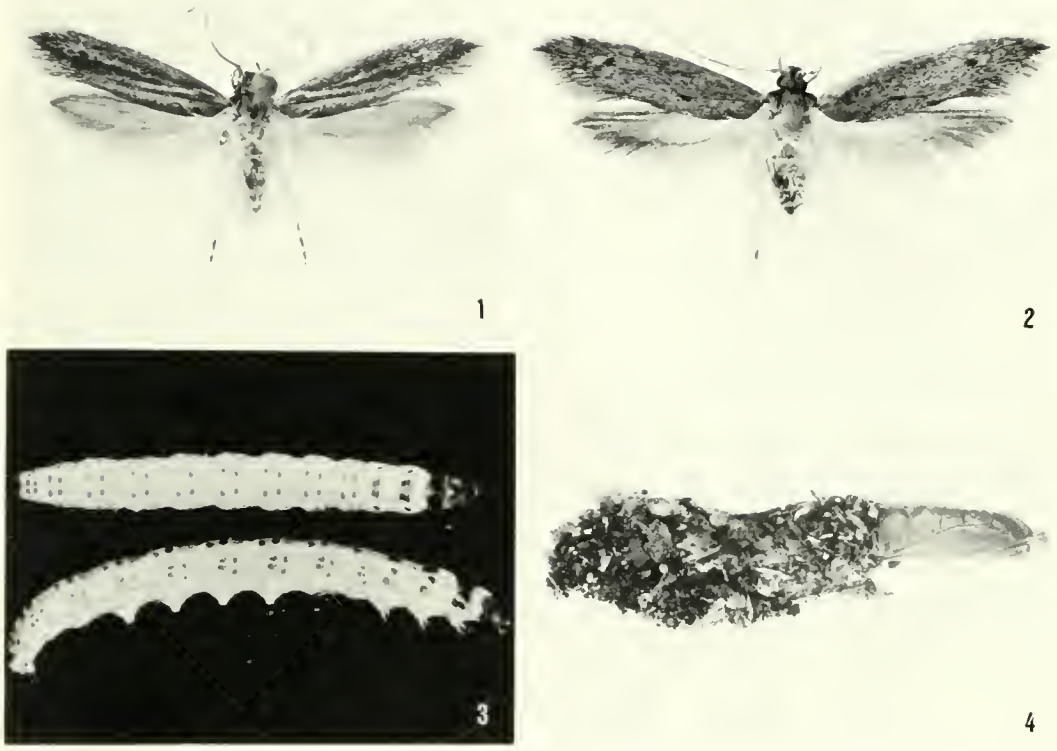
Gelechia ligniferella Walker, 1875: 192.—Durrant, 1925: 12 (synonym of *Hieroxestis subcervinella*).

Laverna plumipes Butler, 1876: 409.—Walsingham, 1907: 713 (synonym of *Opogona subcervinella*); 1919: 259.

Adult (Figs. 1, 2).—Length of forewing: ♂, 7.3–11.2 mm; ♀, 9–12.5 mm. Moderately large, generally dark grayish brown moths with a small, black subapical spot on forewing near apex of discal cell and a similar one at basal third on anal fold; male slightly paler in color with faint longitudinal streaks of light brown or buff.

Head: Vestiture smooth except for a pair of bilateral tufts of erect, pale brown to cream, piliform scales between antennal bases; scales of frons broad, cream colored; vertex covered by a dense row of broad cream scales that curve over frons; caudal portion of vertex with broad, grayish brown scales; occiput light brown with a scattered arch or median patch of dark fuscous scales. Antenna 103–125 segmented, approximately 0.8 the length of forewing; scape cream dorsally, with scattered fuscous scales ventrally; flagellum uniformly covered with small but moderately broad, cream to buff scales arranged in a single row, completely encircling each flagellomere (Fig. 12); sensilla chaetica (with spiral grooves) and trichodea (longitudinal grooves) relatively dense and randomly scattered over each flagellomere; a few pair of sensilla coeloconica located near distal margin (Figs. 13, 14). Pilifers moderately developed with setae nearly meeting at midline (Fig. 9). Labrum densely covered with microtrichia. Mandible vestigial but exceeding pilifer setae in length. Maxillary palpus 5-segmented, elongate, exceeding length of relatively short haustellum; dorsal and lateral surfaces densely covered with cream scales; venter naked with dense sensilla; apex of fifth segment with a slender basiconic sensillum and another slightly smaller one at subapex (Figs. 15, 16). Haustellum with a series of shallow plates over basal half; largest plates with a pair of short sensilla basiconica (Fig. 10). Labial palpus upcurved, smoothly covered with cream scales except for a lateral, subapical series of 3–4 cream bristles and a ventral subapical tuft of 6–8 bristles; third segment with an elongate, narrow sensory pit located just beyond middle (Figs. 17, 18).

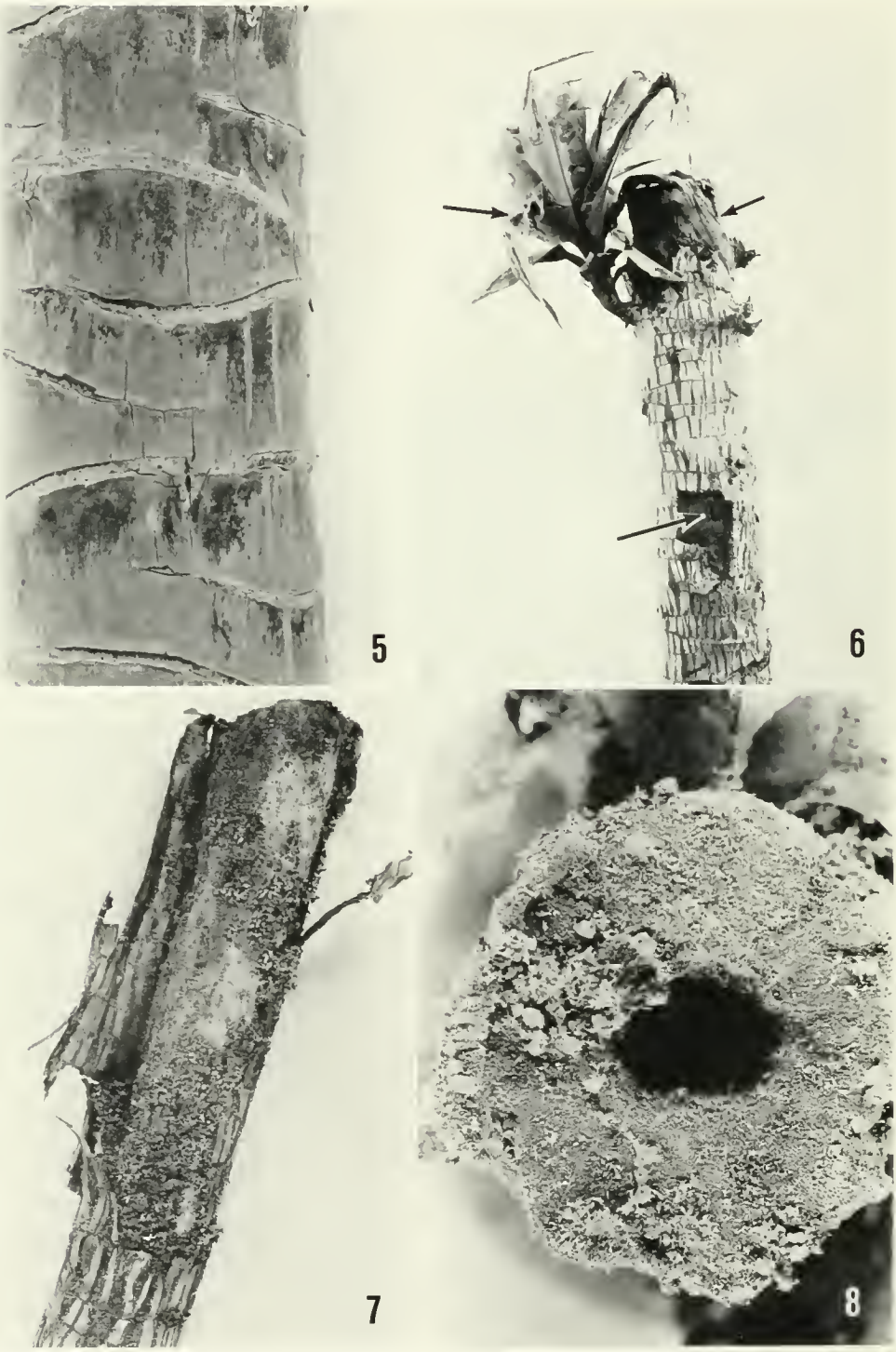
Thorax: Pronotum light brown with heavy to sparse scattering of fuscous scales and usually with a small to large median patch of fuscous on anterior margin and on tegula. Venter uniformly shiny cream. Forewing



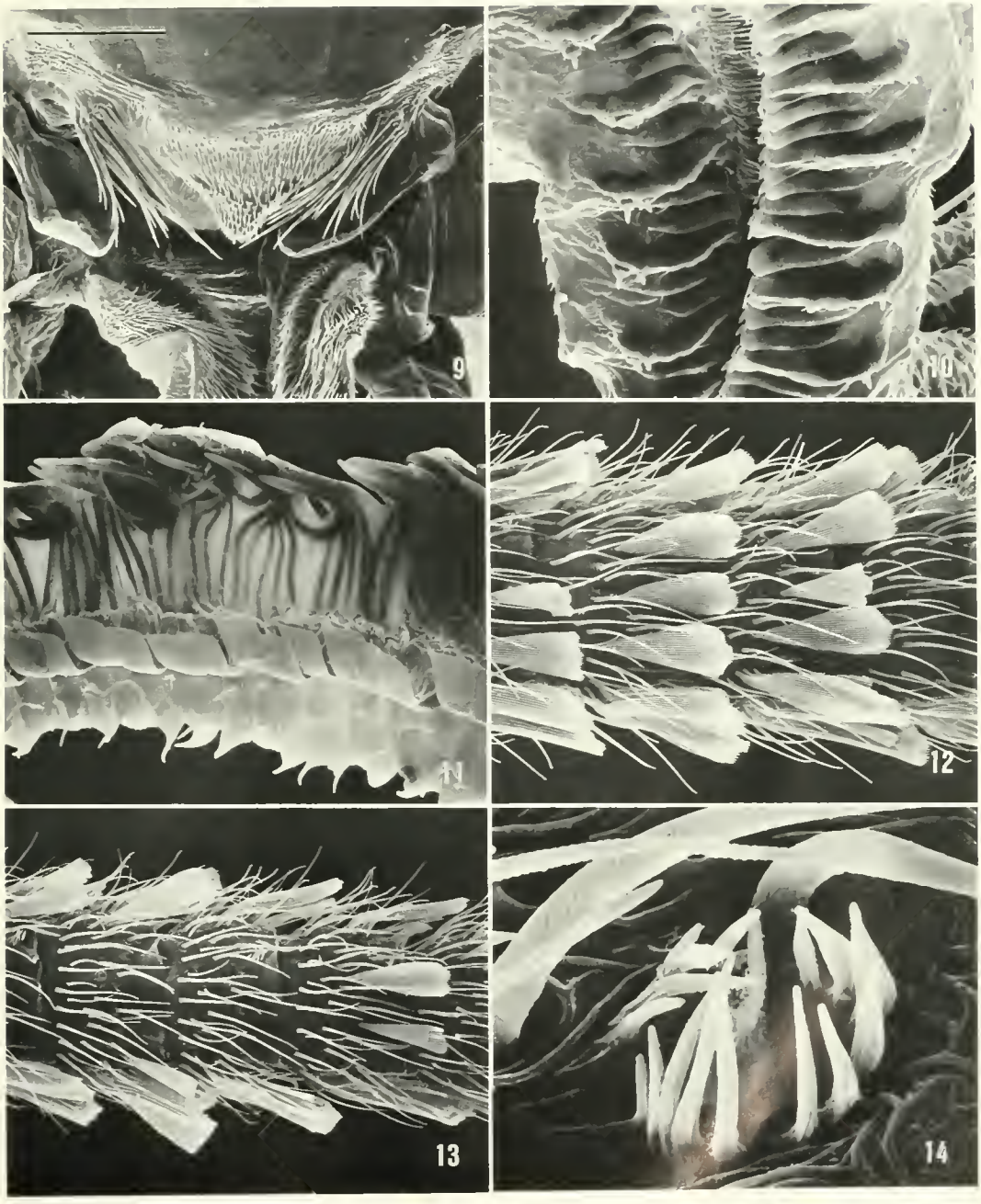
Figs. 1–4. *Opogona sacchari.* 1, Adult male, length of forewing 9.5 mm. 2, Adult female, length of forewing 12.5 mm. 3, Larvae, maximum length 30 mm. 4, Cocoon with pupal exuvium, cocoon length 12.5 mm.

light brown in female with an almost equal amount of scattered dark brown scales; male with dark brown scales more concentrated into longitudinal streaks, particularly evident along upper and lower margins of discal cell; a small, dark fuscous subapical spot near apex of cell and a more elongate fuscous spot along anal fold at basal third in both sexes; male retinaculum a relatively elongate flap from ventral subcostal margin, with apical margin rolled under (Figs. 24, 25). Hindwing light yellowish brown with slender scales in male, more shiny gray and with slightly broader scales in female; male with elongate hair pencil from dorsal base (Figs. 28–30); ultrastructure of pencil sex scales as illustrated (Figs. 31–33); male frenulum a single stout bristle (Fig. 26); female with usually five stout frenular bristles (Figs. 27). Foreleg mostly cream; coxa with a small amount of grayish fuscous suffusion at base; dorsal surfaces of tibia and tarsus heavily suffused with grayish fuscous; normal pectinated epiphysis present (Figs. 19, 20). Pretarsus of all legs normal, with relatively broad unguitractor plate bearing 7–10 ranks of scutes in a single transverse row (Figs. 21–23). Midleg uniformly cream except for slight grayish fuscous suffusion over dorsal surface of tarsus. Hindleg similar to midleg in color except with less grayish fuscous on tarsus and with dense, elongate piliform setae from tibia.

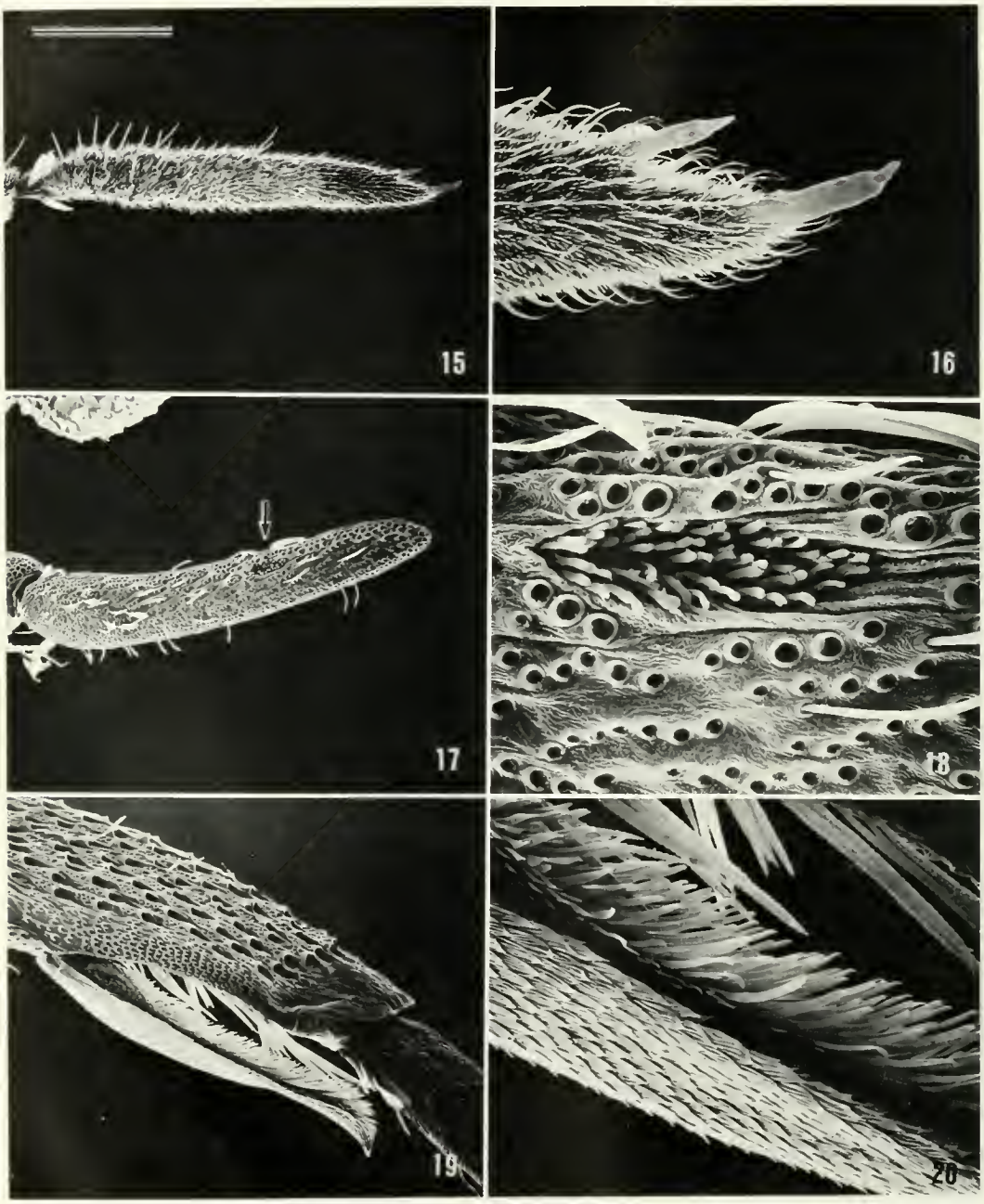
Abdomen: Terga mostly grayish brown with caudal margins and pleura buff to cream colored; venter of female uniformly cream,



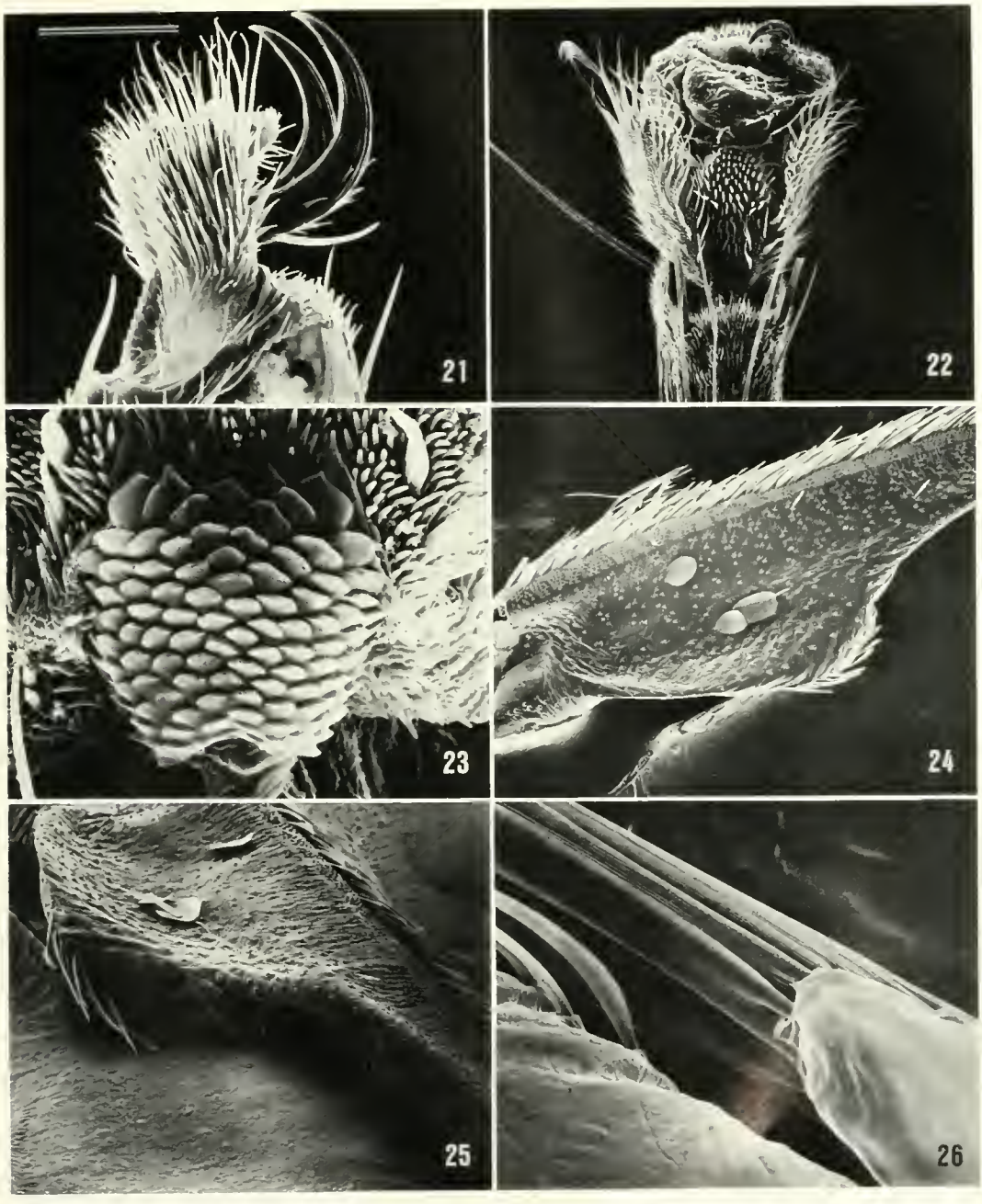
Figs. 5–8. Damage to *Dracaena fragrans* by *Opogona sacchari* larvae (see arrows). 5, Healthy stem. 6–8, Typical feeding damage to *Dracaena fragrans* canes.



Figs. 9–14. *Opogona sacchari*, adult morphology. 9, Labrum, anterior view (100 μm). 10, Base of haustellum (38 μm). 11, Haustellum, food canal (15 μm). 12, Antenna, scale pattern (50 μm). 13, Antenna, sensilla (60 μm). 14, Sensillum coeloconicum of antenna (4.3 μm). (Scale lengths in parenthesis; bar scale for all photographs = Fig. 9.)

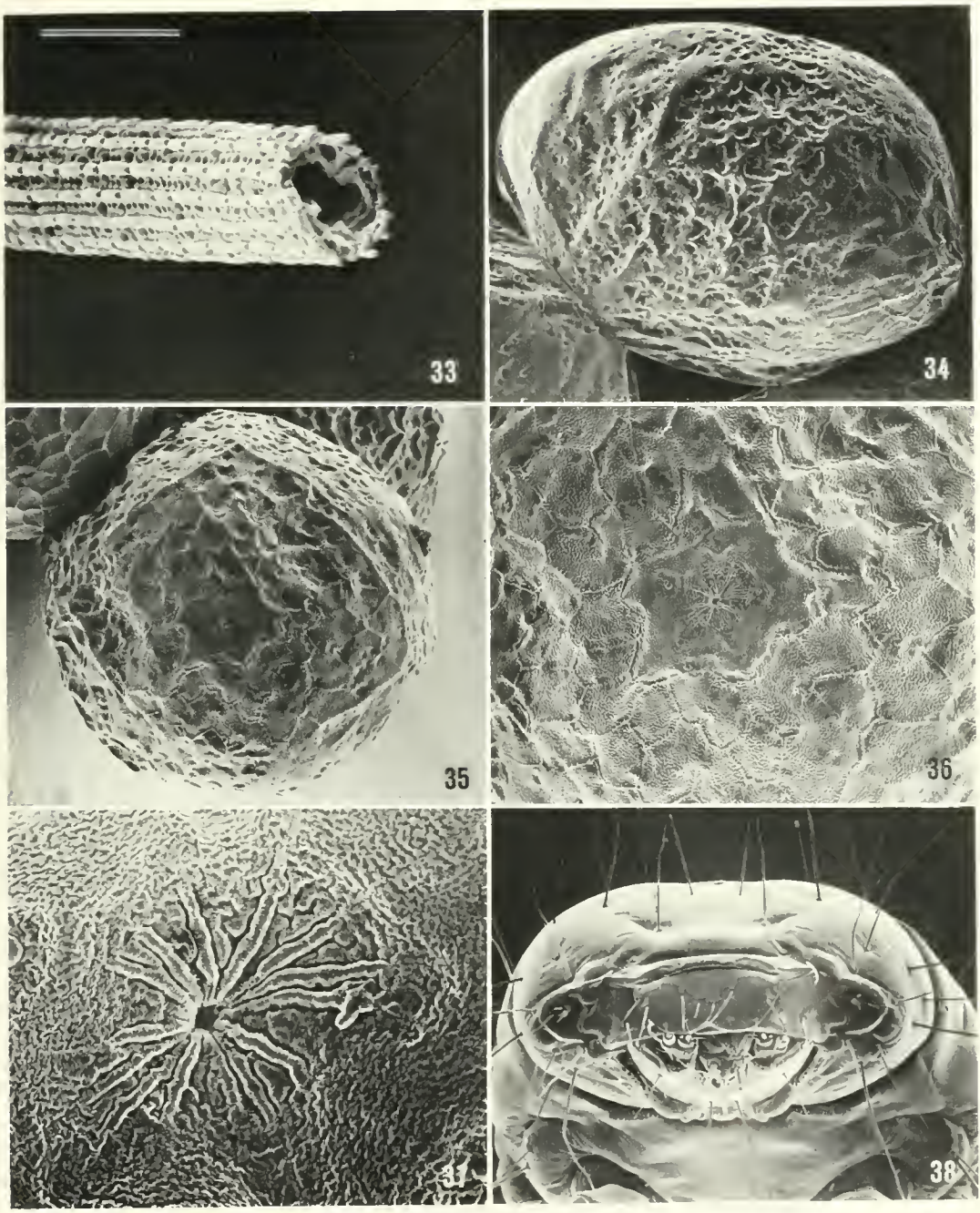


Figs. 15–20. *Opogona sacchari,* adult morphology. 15, Maxillary palpus, apical (fifth) segment (100 μm). 16, Apex of Fig. 15 (23.1 μm). 17, Labial palups, apical (third) segment (176 μm). 18, Detail of sensory pit in Fig. 17 (see arrow) (25 μm). 19, Epiphysis (120 μm). 20, Detail of pecten on epiphysis (27 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 15.)



Figs. 21–26. *Opogona sacchari*, adult morphology. 21, Pretarsus of midleg, lateral view (20 μm). 22, Ventral view (50 μm). 23, Unguitractor plate of pretarsus (7.5 μm). 24, Subcostal retinaculum of male forewing (0.27 mm). 25, Distal-lateral view of Fig. 24 (176 μm). 26, Male frenulum (38 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 21.)

Figs. 27–32. *Opogona sacchari*, wing morphology. 27, Female frenulum (250 μm). 28, Hair pencil of male hindwing, dorsal wing (1 mm). 29, Base of male hair pencil (176 μm). 30, Raised scale sockets of hair pencil (30 μm). 31, Surface ultrastructure of a single hair pencil scale (3.8 μm). 32, Detail of Fig. 31 (1.2 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 27.)



Figs. 33–38. *Opogona sacchari*, adult, egg, and larval morphology. 33, Cross section of hair pencil scale (Fig. 31) (3.8 μm). 34, Egg, lateral view (150 μm). 35, Micropyle (136 μm). 36, Detail of Fig. 35 (75 μm). 37, Detail of central disk (Fig. 36) (17.6 μm). 38, Head of larva, anterior view (60 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 33.)

grayish brown in male; both sexes with a lower lateral series of five dark fuscous spots on A3–7.

Male genitalia (Figs. 79–82): Uncus deeply divided into two large widely separated lobes arising beneath tegumen and bearing numerous stout elongate setae on their mesal surfaces. Tegumen a relatively broad ring dorsally. Vinculum tapering to a broad, relatively truncate saccus. Valva prominently divided into a large, elongate, rounded apical lobe and a much smaller, acute cucullar lobe. Aedoeagus a relatively small, straight, slender tube without cornuti; phallobase much larger and greatly inflated.

Female genitalia (Figs. 83, 84): Tertiary apophyses present in A10. Genital plate moderately divided into a pair of rounded lobes. Corpus bursae with a single large sagitate signum bearing elongate anterior arms.

Egg (Figs. 34–37).—Length, 0.5–0.55 mm; diameter, 0.38 mm; oval in shape, round in cross section; color light yellow at oviposition, gradually becoming yellowish brown prior to eclosion. Surface irregularly pitted. Micropyle consisting of a single, centrally positioned opening with small radiating grooves forming an enlarged, reticulate pattern of low ridges over entire end of egg; reticulations mostly 5–6 sided.

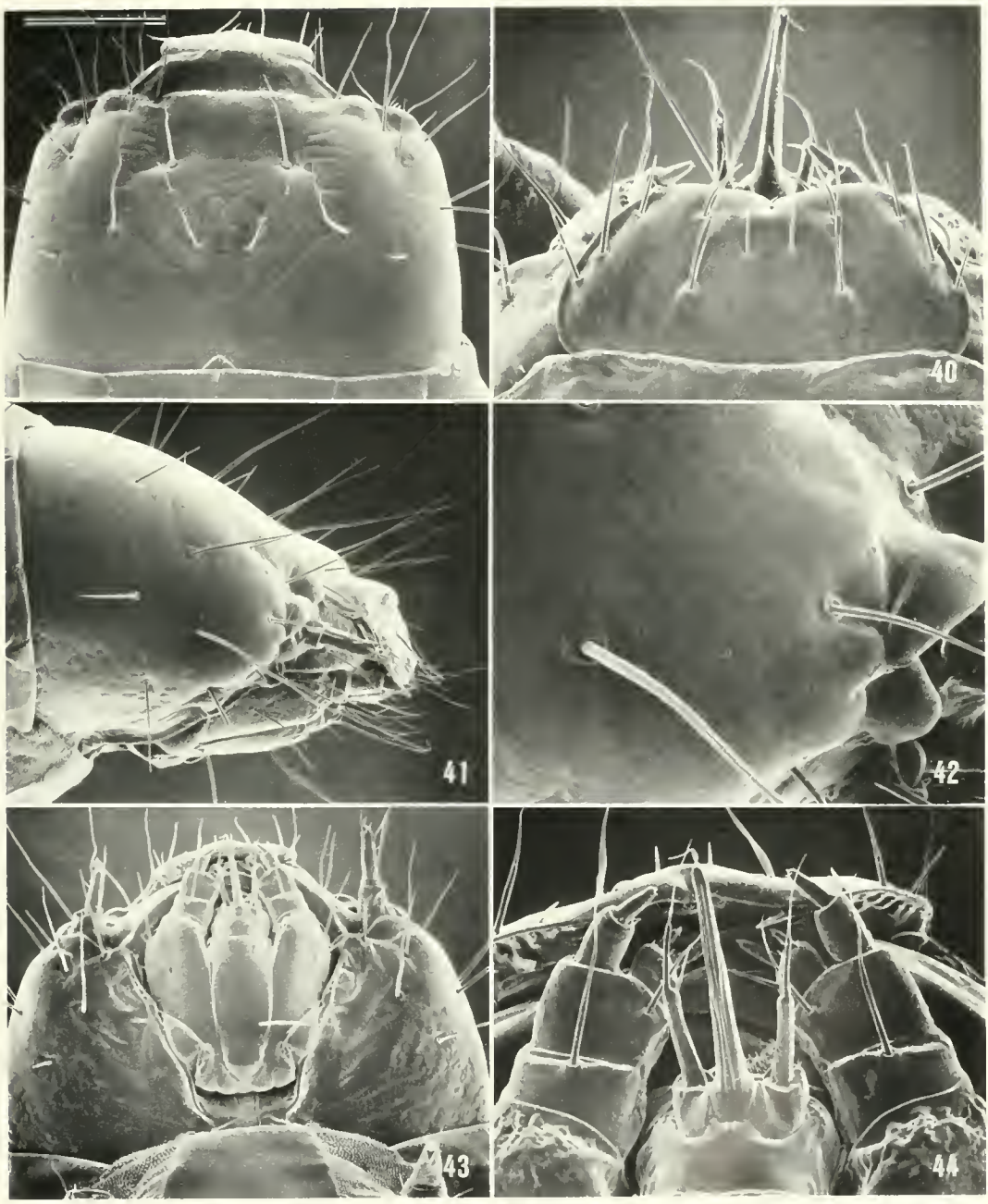
Larva (Figs. 3, 38–66).—Length of largest larva 30 mm, maximum diameter 3 mm. Body generally white with dark brown plates and pinacula.

Head: Maximum width 2.5 mm. Color reddish brown, becoming darker anteriorly and over frons. Chaetotaxy as illustrated. Stemmata rudimentary, consisting of a pair of widely separated, clear lenses, probably corresponding to stemmata 1 and 5; the most anterior (5) located ventral to antennal socket; the most posterior (1) midway between A3 and S2. Mandible with five cusps. Spinneret long and slender with a minute orifice. Labial palpus 2-segmented, elongate and slender, equalling or slightly exceeding length of spinneret; apical seta one-third the length of entire palpus. Apex of mentum with a pair of minute secondary labial setae.

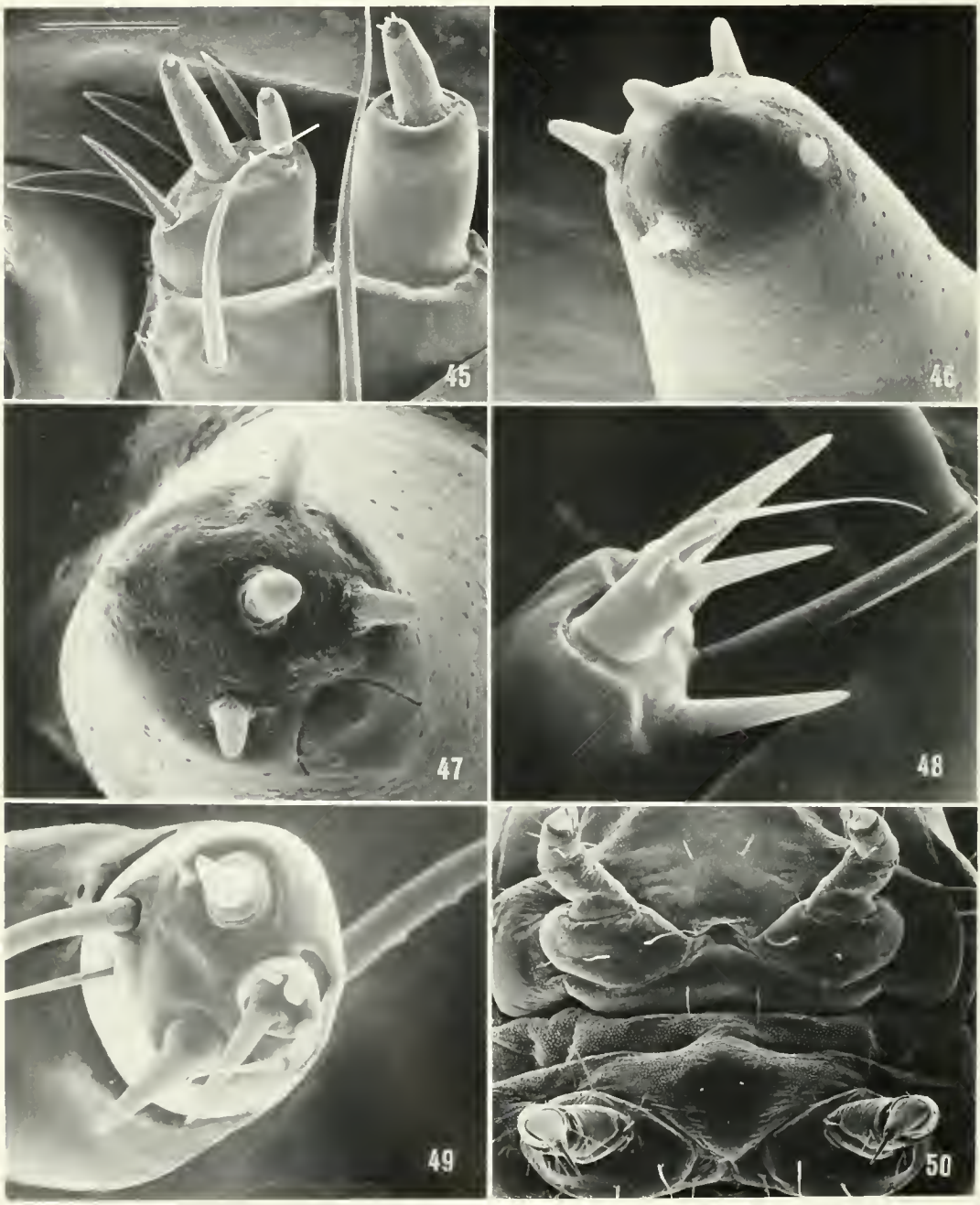
Thorax: Pronotum and spiracular plate dark reddish brown, lighter in color along margins; spiracle together with L setae on same plate. Pinacula over entire body relatively large, dark brown and very distinct on whitish integument. Meso- and metathorax with L2 arising on a separate pinacula from L1 and 3. MSD1 and 2 of similar length and reduced. Legs well developed; tarsal claw elongate; basal lobe actually bilobed and with a minute conical seta from inner angle (Figs. 51, 52).

Abdomen: Whitish in color with brownish pinacula. L2 on separate pinacula from spiracle. Prolegs well developed on A3–6 and 10; crochets A3–6 uniordinal, uniserial, and arranged in a complete ellipse composed of approximately 43–45 hooks; a scattered band of much smaller, numerous spines encircling apex of planta (Fig. 53); crochets on A10 with 20–22 hooks and a dense, scattered band of much smaller spines along anterior edge of planta (Figs. 55, 56).

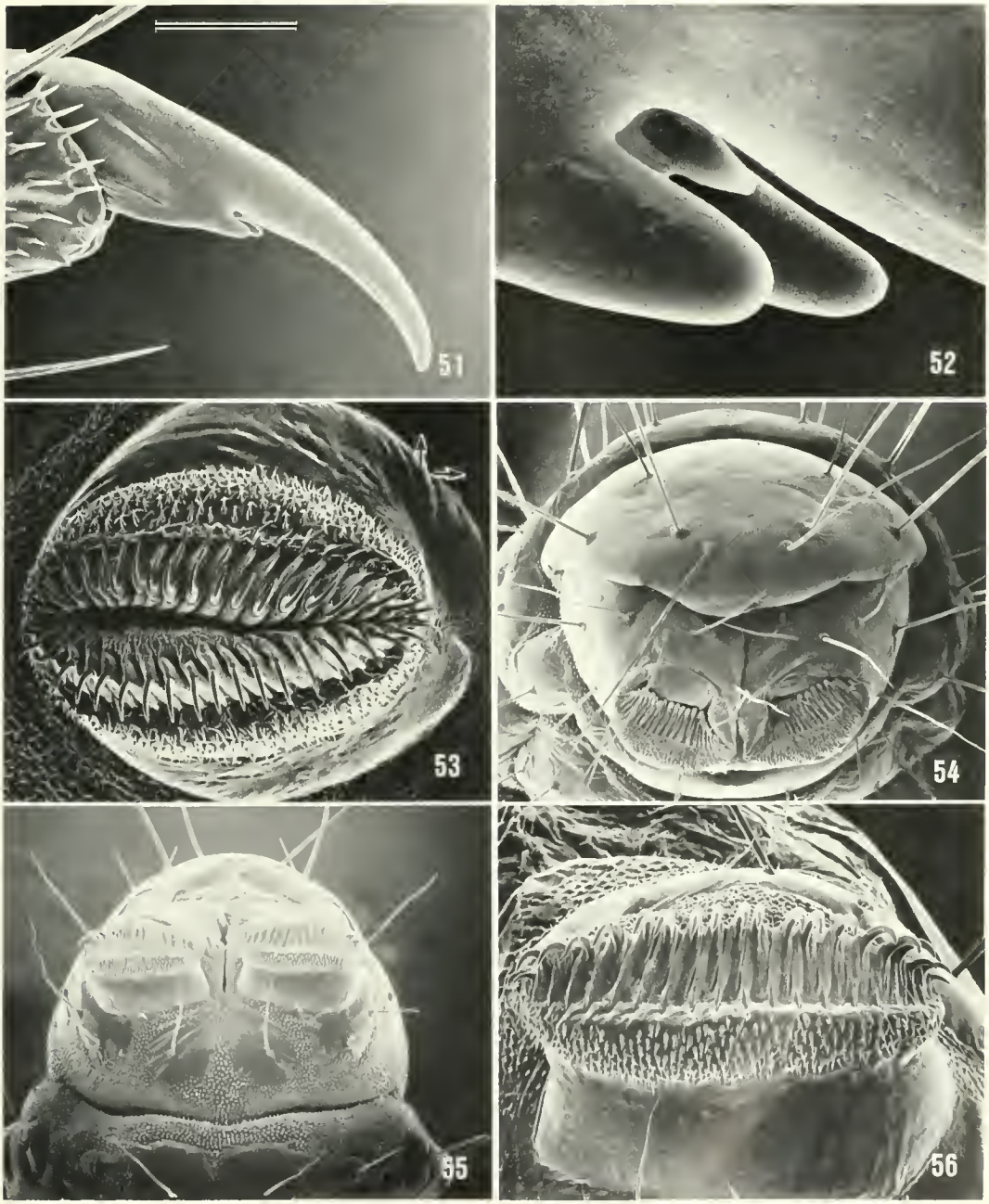
Pupa (Figs. 67, 68).—Length, 9–12.8 mm; maximum width, 2–3.5 mm. Color usually light brown ventrally and dark reddish brown dorsally; wing cases becoming darker with maturity; frontal process, cremaster, and adjacent areas extremely dark, often black. Head with frontal process (cocoon cutter) moderately developed, with a broad, triangular apex (Figs. 68, 78); labrum with a pair of lateral setae. Anterolateral margins of mesonotum with a pair of perforated bands composed of minute, raised slit openings (Figs. 69–71). Forewings extending to middle of A5. Hindlegs to A6. A simple, anterior row of short, stout, dorsal spines present on segments A4–8; tabulation of spines as follow: A4 = 56–70, A5 = 53–72, A6 = 57–71, A7 = 44–50, A8 = 8–18. Last pair (A8) of spiracles on raised, swollen bases (Figs. 74–76). Cremaster consists of a large pair of stout hooks arising dorsally from



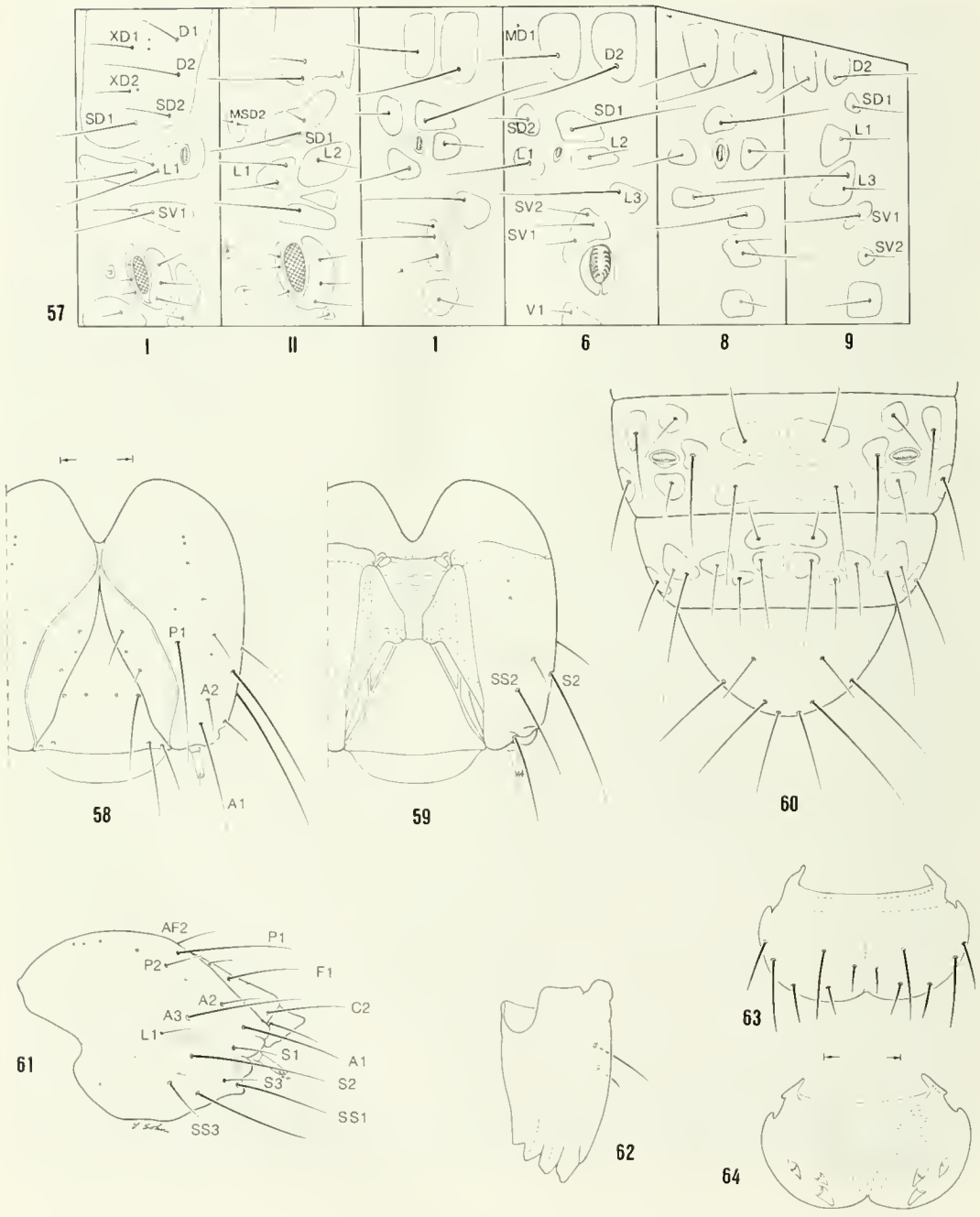
Figs. 39–44. *Opogona sacchari*, larval morphology. 39, Head, dorsal view (0.6 mm). 40, Labrum, dorsal view (176 μm). 41, Head, lateral view (0.43 μm). 42, Stemmal area (136 μm). 43, Head, ventral view (0.5 mm). 44, Maxilla and labium (150 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 39.)



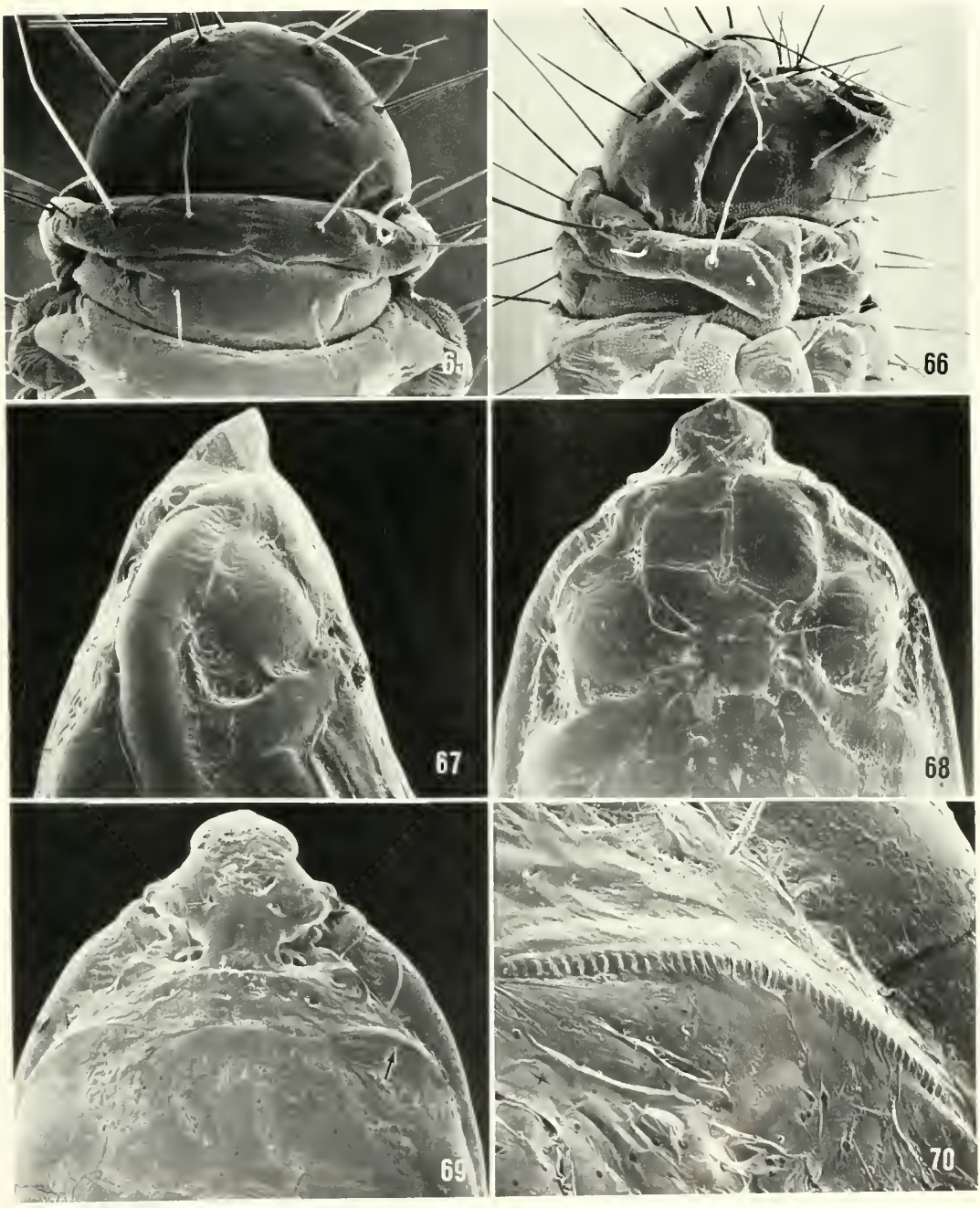
Figs. 45–50. *Opogona sacchari*, larval morphology. 45, Maxilla (60 μm). 46, Apex of maxillary palpus (6 μm). 47, Apex of maxilla (5 μm). 48, Apex of antenna (30 μm). 49, Apex of antenna (27 μm). 50, Ventral view of pro- and mesothorax (0.6 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 45.)



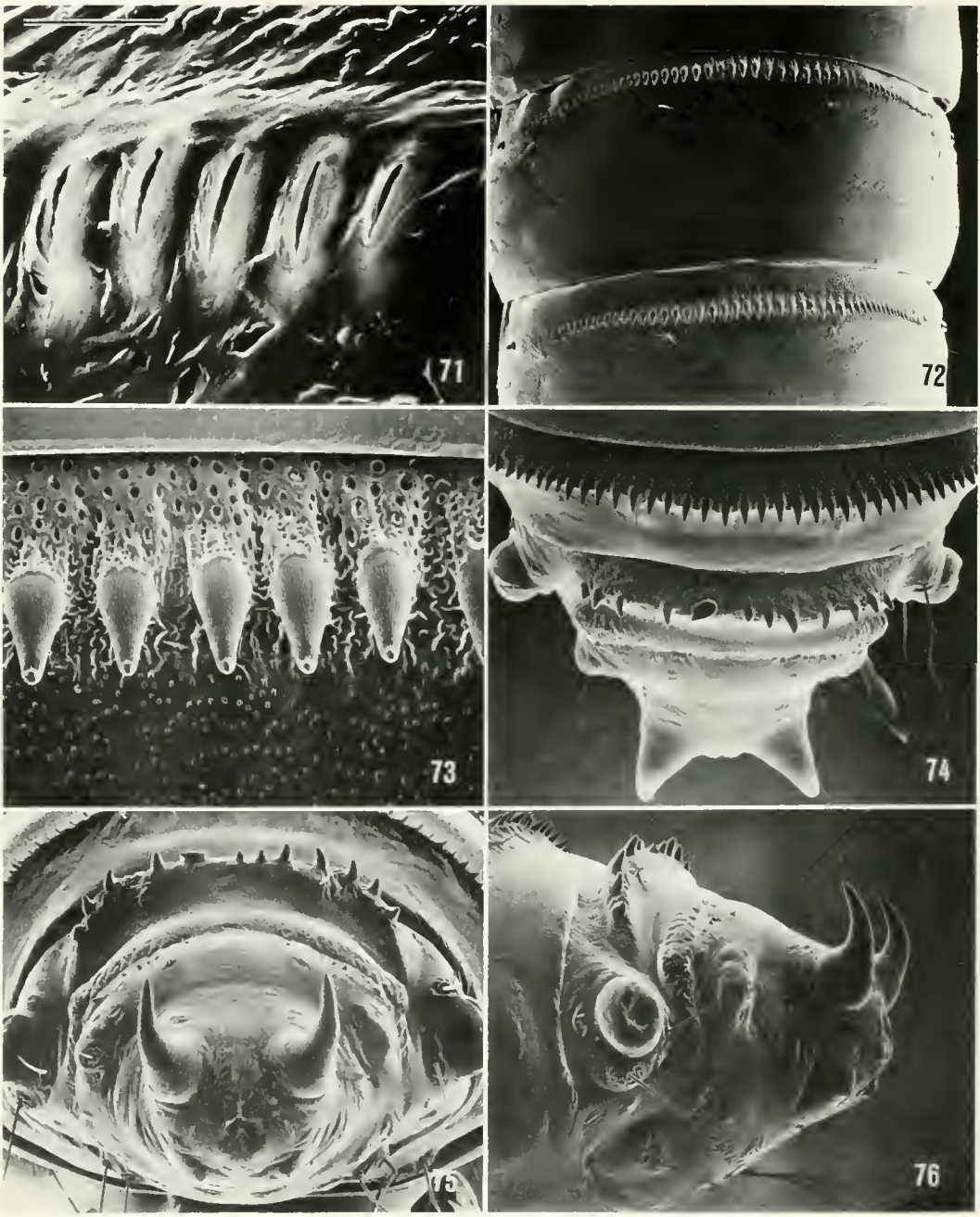
Figs. 51–56. *Opogona sacchari*, larval morphology. 51, Pretarsal claw of prothorax (50 μm). 52, Detail of axial lobes and seta of Fig. 51 (6 μm). 53, Proleg of A3, ↑ anterior, → meson (136 μm). 54, Caudal view last abdominal segment, A10 (0.5 mm). 55, Ventral view, A9, 10 (0.5 mm). 56, Anal proleg, A10 (150 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 51.)



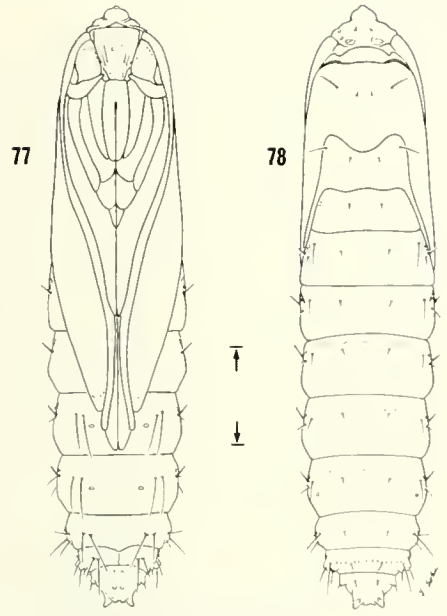
Figs. 57–64. *Opogona sacchari*, larval chaetotaxy. 57, Body segments T1–2, A1, 6, 8–9. 58, Head, dorsal view (0.5 mm). 59, Ventral view. 60, Segments A8–10, dorsal view. 61, Head, lateral view. 62, Mandible. 63, Labrum, dorsal view (0.25 mm). 64, Ventral view. (Scale lengths in parentheses.)



Figs. 65–70. *Opogona sacchari*, larval and pupal morphology. 65, Larval segments A8–10, dorsal view (0.6 mm). 66, Lateral view of Fig. 65 (0.6 mm). 67, Pupa, lateral view of head (0.6 mm). 68, Ventral view of Fig. 67 (0.6 mm). 69, Dorsal view of Fig. 67, perforated band (see arrow) (0.6 mm). 70, Detail of dorsal perforated band (136 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 65.)



Figs. 71–76. *Opogona sacchari*, pupal morphology. 71, Detail of openings in perforated band (see Fig. 69) (15 μm). 72, Dorsum of A4–5 (0.75 mm). 73, Dorsal spines of A4 (100 μm). 74, Dorsal view of A7–10 (0.5 mm). 75, Caudal view of A8–10 (0.5 mm). 76, Lateral view of A8–10 (0.5 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 71.)



Figs. 77, 78. *Opogona sacchari*, pupa. 77, Ventral view (2 mm). 78, Dorsal view. (Scale lengths in parentheses.)

A10 (Figs. 74–76); a much smaller pair of conical tubercules also present ventrally.

Pupation occurs in a cocoon (Fig. 4) of white silk usually covered with dark frass and plant debris, 14–18 mm long, 3–4 mm in diameter. Normally, the cocoon is constructed somewhere in or near the feeding site.

Types.—Syntypes ♂, ♀, deposition unknown (*sacchari*); Holotype, BMNH (*subcervinella*); syntypes, ♂, ♀, BMNH (*sanctaehelenae*); holotype, sex unstated, BMNH (*ligniferella*); syntype(s)?, sex and number of specimens unstated, BMNH (*plumipes*).

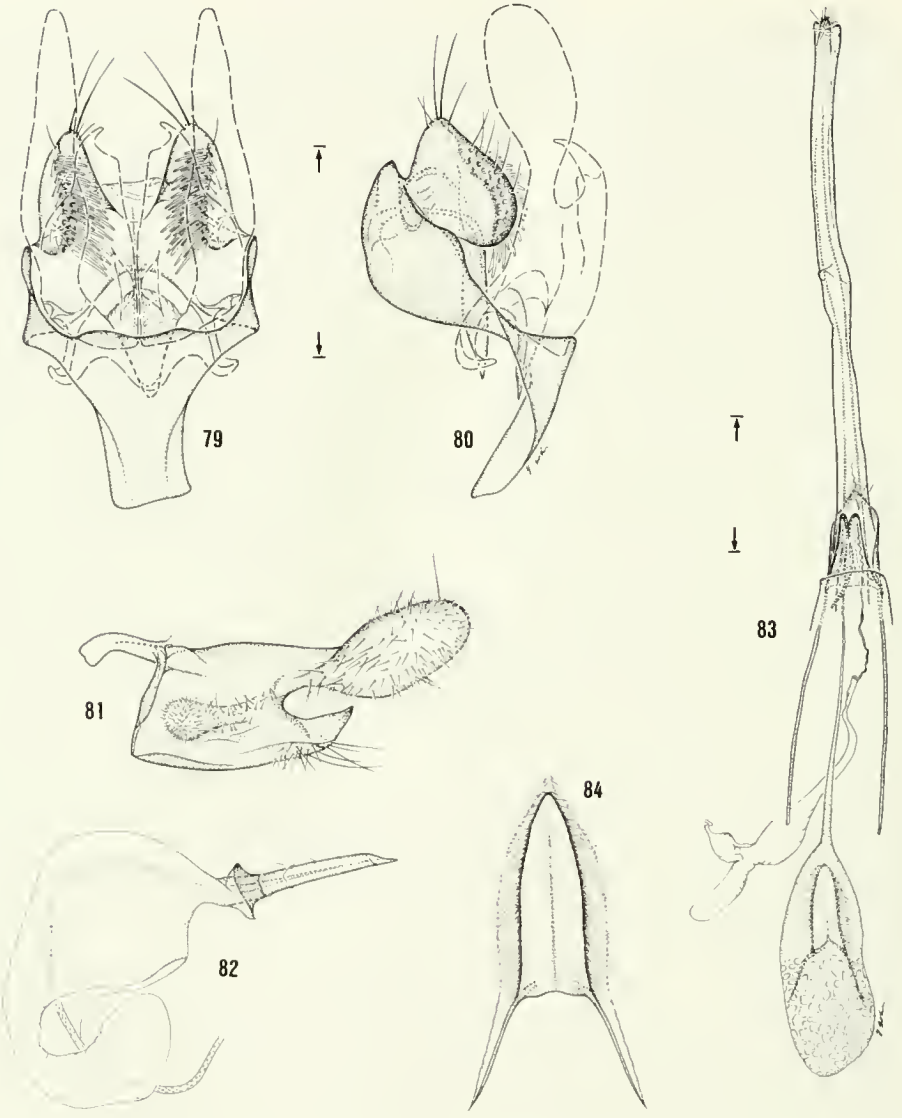
Type localities.—Mascarene Islands: Mauritius (*sacchari, subcervinella*), St. Helena (*sanctaehelenae, ligniferella*); Mascarene Islands: Rodriguez (*plumipes*).

Hosts.—46 plant hosts reported (see Table 1).

Distribution (maps 1, 2).—A widely ranging, partly pantropical species, early reported from several circum-African islands (Canary Islands, St. Helena, Mauritius, Rodriquez and the Seychelles), as well as South Africa; frequently intercepted in several European countries (Belgium, France, Great Britain, Greece, and the Netherlands). More recently, *O. sacchari* has been introduced into South America and the West Indies, including Bermuda, and is now established in nurseries over much of southern Florida.

Discussion.—By its relatively large size and predominantly brown color, *Opogona sacchari* is easily distinguished from nearly all other members of this large complex. Its affinities are with *O. omoscopa* (Meyrick) as suggested by their similar male genitalia and shared presence of a dorsal hair pencil in the hindwings of the male. Present evidence suggests that this complex of obviously related species warrants recognition under and resurrection of the currently synonymized genus *Hieroxestis*. Hopefully this and similar generic uncertainties can be resolved following a revision of the large cosmopolitan genus *Opogona*. The larva of *O. sacchari* may be recognized by the presence of two stemmata, separation of the spiracle from the pinaculum bearing L2 on the first eight abdominal segments, by the large number of crochets (A3–6 = 43–45, A10 = 20–22), and by complete encirclement of the abdominal planta by a band of small, secondary spines. In *O. omoscopa*, a pantropical species recently introduced into California (Davis 1978), only one anterior stemma has been observed, the first eight abdominal spiracles are united with L2 on a common pinaculum, the crochets are fewer in number, and the abdominal planta A3–6 have spines only along the anterior margin. The pupae of these two species are also similar but may be distinguished by the raised spiracle on A8 and larger cremaster spines of *O. sacchari*.

A peculiar structure of unknown function in the pupa of this species deserves further comment. It consists of a bilateral pair of perforated bands curving around the anterolateral margins of the mesonotum (Figs.



Figs. 79–84. Adult genitalia. 79, Male, ventral view (0.25 mm). 80, Lateral view. 81, Lateral view of valva. 82, Aedoeagus, lateral view. 83, Female, ventral view (1 mm). 84, Detail of signum in Fig. 83. (Scale lengths in parentheses.)

69–71). The bands are narrow and elongate and under high magnification can be observed to comprise raised, slitlike openings. The senior author has not noted this in other species, perhaps because the bands were simply overlooked. Possibly their function is merely to weaken the cuticle, thereby facilitating rupture of the pupal shell during eclosion. The band was observed to have been expanded or further separated in most pupal exuviae examined, although the major breaks in this region of the pupal shell during ecdysis did not occur through the perforated bands but were located anterior to the pronotum and down the mid-dorsal line of the pro- and mesonotum.

Table 1. Plant hosts of *Opogona sacchari*.

Plant Species	Reference	Country
Agavaceae		
Cordyline terminalis (L.) Kunth	Heppner et al. 1987	United States
Dracaena fragrans (L.)	Declercq and Van Luchene 1977	Belgium
Dracaena fragrans (L.) Ker-Gaus, "var. *massangeana*"	Heppner et al. 1987	United States
Dracaena marginata Lam.	Heppner et al. 1987	United States
Dracaena reflexa Lam.	Heppner et al. 1987	United States
Yucca elephantipes Regel	Heppner et al. 1987	United States
Yucca sp.	Heppner et al. 1987	United States
Araceae		
Colocasia esculenta Schott.	Cintra 1975	Brazil
Philodendron scandens Lindl.	Süss 1974	Italy
Araliaceae		
Polyscias fruticosa (L.) Harms	Heppner et al. 1987	United States
Polyscias fruticosa (L.) Harms, "elegans"	Heppner et al. 1987	United States
Asteraceae		
Dahlia sp.	Cintra 1975	Brazil
Bromeliaceae		
Aechmea fasciata (Lindl.) Baker	Süss 1974	Italy
Aechmea fasciata (Lindl.) Baker "Variegata"	Süss 1974	Italy
Guzmania lingulata var. × *magnifica* [Hort.]	Süss 1974	Italy
Nidularium tricolor [species name unknown, possibly = *Neoregelea* 'Perfecta Tricolor,' a cultivar]	Süss 1974	Italy
Caricaceae		
Carica papaya L.	Viette 1951	Madagascar
Convolvulaceae		
Ipomoea batatas Lam.	USNM (new record)	Peru
Cycadaceae		
Cycas revoluta Thunberg	Heppner et al. 1987	United States
Dioscoreaceae		
Dioscorea sp.	Heppner et al. 1987	United States
Gesneriaceae		
Gloxinia sp.	Süss 1974	Italy
Saintpaulia sp.	Süss 1974	Italy
Iridaceae		
Gladiolus sp.	Cintra 1975	Brazil
Leguminosae		
Albizia julibrissin Durazz.	Heppner et al. 1987	United States
Enterolobium sp.	Heppner et al. 1987	United States
Erythrina variegata L.	FSCA (new record)	United States
Liliaceae		
Sansevieria laurantii Wildem.	Süss 1974	Italy
Sansevieria trifasciata laurentii Wildem.	Declercq and Van Luchene 1977	Belgium
Malvaceae		
Hibiscus sp.	Moreton 1974	Great Britain

Table 1. Continued.

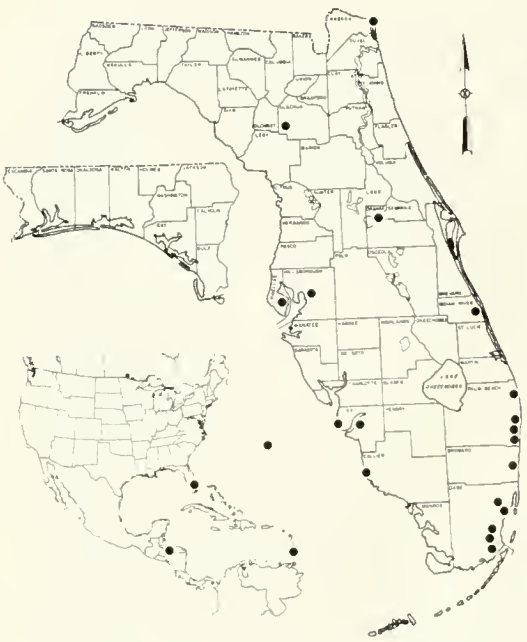
Plant Species	Reference	Country
Marantaceae		
Maranta leuconeura massangeana Schum.	Süss 1974	Italy
Stromanthe sanguinea Sonder	Süss 1974	Italy
Moraceae		
Ficus elastica (H. A. Siebrecht)	Moreton 1974	Great Britain
Musaceae		
Musa cavendishii Paxt	Oldham 1928	Canary Islands
Musa paradisiaca L.	Heppner et al. 1987	United States
Musa sapientum L.	Oldham 1928	Canary Islands
Strelitzia sp.	Zandvoort 1972	Netherlands
Orchidaceae		
"Orchids"	Heppner et al. 1987	United States
Palmae		
Arecastrum sp.	Heppner et al. 1987	United States
Bactris [= *Guilielma*] *gasipaes* HBK	Heppner et al. 1987	United States
Chamaedorea elegans Mart.	Heppner et al. 1987	United States
Chamaedorea erumpens H. E. Moore	Heppner et al. 1987	United States
Chamaedorea seifrizii Burret	Heppner et al. 1987	United States
Poaceae		
"Bamboo"	Oldham 1928	Canary Islands
Saccharum officinarum L.	Bojer 1856	Mauritius
Zea mays L.	Oldham 1928	Canary Islands
Solanaceae		
Capsicum sp.	Süss 1974	Italy
Solanum melongena L. var. *esculentum* Nees	Süss 1974	Italy
Solanum tuberosum L.	Oldham 1928	Canary Islands
Verbenaceae		
Clerodendrum sp.	Heppner et al. 1987	United States

Biology

The larvae of most species of *Opogona* for which we have information are detritus feeders and rarely feed on living plant tissue. *Opogona sacchari* thus departs from the norm and can be a serious pest of banana, maize, potato, sweet potato, sugar cane, and certain greenhouse crops (Alam 1984, Durrant 1925, Oldham 1928, Süss 1975, Veenenbos 1981). A total of seven instars are indicated, based on head capsule measurements of larvae reared on artificial diet (Table 2). All measurements were based on pooled data for both sexes. The discreteness of the last two instars as interpreted from head capsule measurements presumably would be better had males only or females only been used. The SD values do not overlap as it is, so likely the conclusion reached as to instar number is correct. More precise data, however, might have shown indication of variation in instar numbers, which seems likely in a generalist feeder of this sort.

Oldham (1928) observed that *O. sacchari* larvae feed on nearly all parts of the banana plant except the roots and leaf blades. Larvae accepted leaves as a food in rearings but normally avoided this part of the plant in nature. The most serious damage occurred in the banana inflorescence. Larvae seldom feed exposed but burrow into the substra-

Map 1. Reported occurrence of *Opogona sacchari*.



Map 2. Distribution of *Opogona sacchari* in Florida (after Heppner et al. 1987).

tum. Their presence is usually indicated by the accumulation of frass and other debris entangled in larval silk over the surface of the injury. The larvae are voracious feeders and construct long meandering galleries through the injury site.

Reports of larval damage on sugar cane has varied markedly. On Barbados, Alam (1984) noted extensive damage to live sugar cane, exceeding that caused by *Diatraea saccharalis* (F.). The young larvae feed under the leaf sheaths and, as they mature, penetrate the stalks and destroy the cane tissue. Infested stalks are hollowed out and gradually filled with larval frass. As in the case on banana, pupation occurs at the feeding site inside the stalks. At the infestation sites studied by J. E. Jones (in litt.), also on Barbados, *O. sacchari* was most abundant in dead or dying stumps and dead canes, suggesting they moved in following an infestation by *Diatraea*. Jones also found that the high incidence of *Opogona* on green canes was associated with a high infestation

Table 2. Larval head capsule width for 7 instar groupings of *Opogona sacchari* (Bojer).

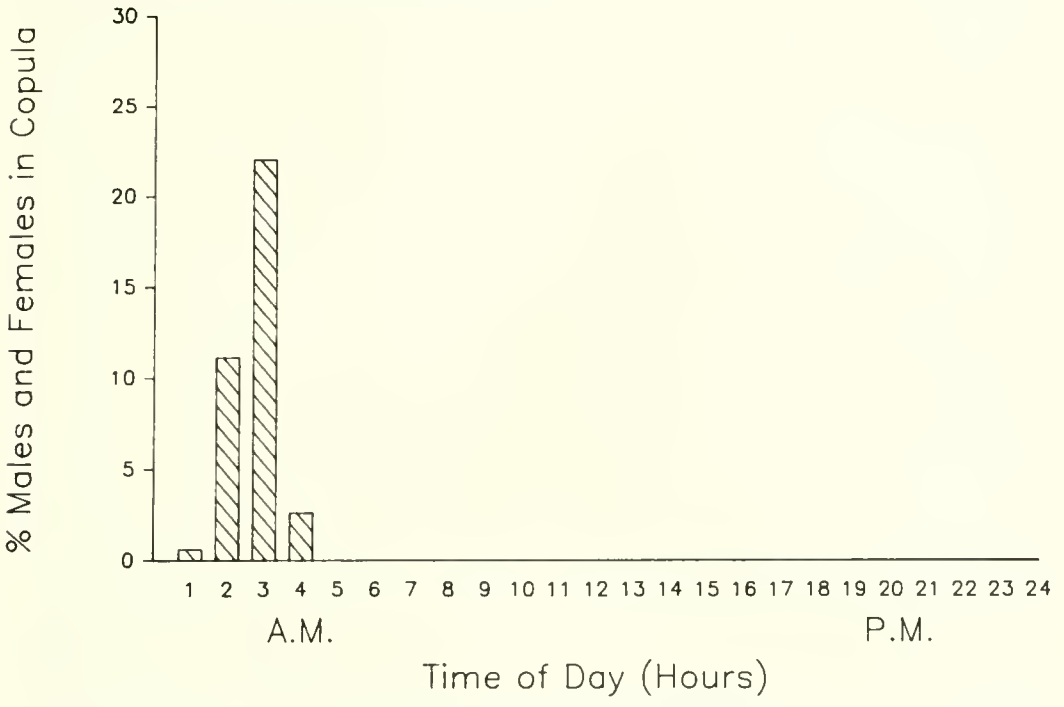
Instar	N	Range (mm)	Mean ± SD (mm)	Ratio of Increase
1	26	0.16–0.24	0.18 ± 0.03	
2	20	0.26–0.32	0.31 ± 0.02	1.72
3	27	0.36–0.56	0.49 ± 0.01	1.51
4	20	0.58–0.88	0.91 ± 0.02	1.85
5	20	0.91–1.16	1.02 ± 0.04	1.12
6	20	1.20–1.44	1.42 ± 0.04	1.39
7	32	1.52–2.56	2.17 ± 0.04	1.42
			Average	1.52

of *Diatraea*, again suggesting that *O. sacchari* invades burrows previously created by *Diatraea*. Thus, the observations by Jones agree most closely with those originally reported by Bojer (1856).

Observations in Florida

A laboratory colony of *O. sacchari* was initiated in 1985 with larvae and pupae collected from infested *Dracaena* canes found at a nursery in Homestead, Florida. Pupae were held individually in 36 ml diet cups until eclosion. Emerging adults were sexed and 17 pairs were placed in 11 cm × 14.5 cm plastic oviposition chambers along with folded filter paper. Adults were provided honey and water. Pairs were held until the female died, males were replaced as needed. The preoviposition period, fecundity and longevity of females and the time required for egg to hatch were determined. First instars were gathered from the oviposition chambers and placed on one of 3 artificial diets in an attempt to rear this species in the laboratory. The 3 diets used were: velvet bean caterpillar diet (VBC), sugar cane borer diet, and the elm spanworm diet (Fedde 1974). All rearing and diet tests were conducted in a rearing room with a photoperiod of 12:12 (L:D) (0600 to 1800 photophase), temp 24 ± 2°C, and RH 65–70%. Larvae were collected at different days from the diet, and preserved in a 70% alcohol for later measurement of head capsule width. Larvae

Table 3. Mating activity of moths in rearing chamber.



were checked daily for onset of pupation and pupal development time was recorded for 175 pupae.

Emerging adults were also placed in 53 × 53 × 50 cm screen cages with *Dracaena* and *Chamaedorea* potted plants. Number of eggs and oviposition site on each plant species was inspected daily.

Results and Discussion

Based on laboratory observations, development of an *Opogona* generation required 50–70 days. More eggs were present on unexpanded leaves and stems than on expanded leaves. Eggs are laid singly or in groups up to 328. They are light yellow at oviposition, turn a dark yellow color ca. 2 days later, and finally yellowish brown prior to eclosion. Eggs hatched in 7.02 ± 0.02 days at 24°C in the laboratory. The preoviposition period for newly emerged females in the laboratory was 1.66 ± 0.14 days at 25°C. Female longevity ($\bar{x}$ ± SD, n = 20) in the laboratory was 9–17 days with a mean of 11.45 ± 0.72 days. Sixty first instar larvae were placed individually on each of the 3 diets tested. Survivorship on the artificial diet was low with the exception of velvet bean caterpillar diet. The highest percentage survivorship, 83%, was on VBC diet.

Experiments were conducted to monitor *O. sacchari* sexual activity throughout the night. Sets (n = 30) of 2–3-day-old virgin males and females were placed in petri dishes (9 cm in diameter) with water and honey as source of food. Each set was placed in an environmental chamber (LD 12:12, 24 ± 2°C, 75–80% RH). The experiment was replicated 4 times. Diel activity was monitored hourly from 6:00 pm to 7:00 am. The period of activity occurred between 1:00 am to 4:00 am. No sexual activity was observed before 1:00 am or after 4:00 am. Through this experiment it became apparent that the op-

timal response period for *O. sacchari* occurs 3 h before the end of scotophase (darkness) (Table 3).

The pupal stadium of larvae placed on VBC diet lasted 12.53 ± 0.33 days. The average weight of pupae was 0.043 g. Table 2 lists a 7 instar model which best fits the data according to Dyar's rule (Dyar 1890). As noted previously, these measurements are based on pooled data for unsexed larvae.

Typical damage of *O. sacchari* on *Dracaena* is characterized by removal of the bark and phloem. Cuttings of *Dracaena* having *Opogona* larvae show exterior debris and frass (Figs. 7, 8) deposits, and have internal feeding damage on dead and living portions of the cortex, pith, roots and leaves (Fig. 6). Damage is not evident 4–6 weeks after infestation. Typical damage to *Chamaedorea* palms can be observed 2–3 weeks after infestation. Each larva feeds at the base and roots of *Chamadorea*, and frass accumulates at the plant base from feeding into roots and petioles. In palms the leaf blades of the growing point become bleached and necrotic.

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REVISION OF *HOCKERIA* WALKER IN THE NEARCTIC REGION WITH DESCRIPTIONS OF MALES AND FIVE NEW SPECIES (HYMENOPTERA: CHALCIDIDAE)

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Abstract.—The genus *Hockeria* Walker is revised for the Nearctic region. Nine species are recognized; five new species (***hainesi***, ***bicolor***, ***brevipennis***, ***micra***, and ***burksi***) are described. Four previously described species, *eriensis* (Wallace), *rubra* (Ashmead), *tenuicornis* (Girault), and *unipunctatipennis* (Girault), are diagnosed and discussed. Males of all species are described and allotypes or plesiotypes designated. *Hockeria americensis* (Girault) is designated a junior synonym of *H. unipunctatipennis*. A key to the Nearctic species for both males and females is presented. Characters of females and males are illustrated. Biological and distributional information is summarized for each species. *Hockeria eriensis* and *H. bicolor* n.sp. are recorded from the Neotropical region.

Key Words: Insecta, *Hockeria*, Chalcididae, revision, new species, Nearctic

The worldwide genus *Hockeria* Walker contains about thirty described species. Walker described *Hockeria* in 1834 with *H. bispinosa* Fabricius, a European species (synonym of *H. bifasciata* Walker), as the nominal type-species. Major faunal treatments of *Hockeria* include: Japan (Habu 1960, 1962), Europe (Boucek 1951), USSR (Nikolskaya 1952, 1960), the Near East and India (Husain and Agarwal 1982). Husain and Agarwal (1982) presented a key to the world species of *Hockeria* but none of the Nearctic species were included. The Nearctic *Hockeria* are revised herein for the first time. No taxonomic keys or comprehensive treatments exist for this fauna. The fauna contains nine species, five of which are newly described in this paper. Past literature on Nearctic *Hockeria* is cataloged in Peck (1963), Burks (1979), and DeSantis (1979).

Hockeria are small to moderate sized wasps (2 to 10 mm). Females have slender filiform antennae and are entirely black, red or orange, or commonly with a combination of red or orange and black. Males have robust filiform antennae, are usually black with some orange markings, and are more robust than females. The forewing of females is clouded in a specific pattern whereas in males it is usually clear.

At present, a generic revision of the American Chalcididae is underway (Boucek, pers. comm.); therefore, a generic description of *Hockeria* is omitted. However, to facilitate the identification of this genus for the Nearctic region the following characters are diagnostic: vertex not produced into horns, hindtibiae truncate distally, two apical hindtibial spurs present (Haltichellinae); marginal vein on anterior margin of forewing, postmarginal and stigmal veins present (Haltichellini); tergite 1 without carinae; posterior margin of scutellum without a median tooth; frontal carina weak, not joining in ocellar area to form an arch.

Useful species characters for females in-

clude: clouded pattern of the forewing; color; shape of the abdomen, hindfemora, head, antennae, and ovipositor sheath; sculpture of tergite 1 and mesopleural acetabulum; length of flagellomeres; body length; and body sculpture. Characters for males include: body length and color; T1 sculpture; forewing clouding and color; shape of the scutellum (especially the shape of teeth on the posterior margin or their absence), flagellomeres, and propodeal carinae.

The taxonomy of the Nearctic *Hockeria* has been based on females, and only the male of *H. eriensis* (Wallace) has been described. Strong sexual dimorphism and dichromatism makes the male-female associations difficult. Males usually have a robust body, robust filiform antennae, clear wings, and black body coloration; whereas, females usually have a more slender body, slender filiform antennae, clouded wings, and red-orange and black body coloration. Species exhibiting strong sexual dimorphism and dichromatism include: *eriensis*, *rubra* (Ashmead), *tenuicornis* (Girault), *unipunctatipennis* (Girault), and *hainesi* n. sp. The species *micra* n. sp., *burksi* n. sp., *bicolor* n. sp., and *brevipennis* n. sp. are less dichromic. Males are similar morphologically, which complicates the task of distinguishing them and making the proper female association. However, examination of large series has permitted the male-female association for all species. These males are described and specimens designated as allotypes or plesiotypes.

The nine Nearctic species will not be classified into species groups at this time. I think a world overview is necessary to determine and designate species groups. However, two species (*H. eriensis* and *H. bicolor* n. sp.) form a unique group separate from other Nearctic species in having a narrow head, globose abdomen, and strongly arched scutellum. Boucek (1951) also noted short, stout forms and slim forms in the European fauna.

World literature denotes a wide range of hosts for *Hockeria*: antlion larvae (Neuroptera), elasmid and tenthredinid pupae (Hymenoptera), free-living Strepsiptera, dipteran pupae, and commonly lepidopteran larvae and pupae (Boucek 1951, Habu 1962, Burks 1979, Narendran and Rao 1987). Hosts have been determined for six of the nine Nearctic species, including three economically important lepidopterous pests: the Western Grapeleaf Skeletonizer (*Harrisina brillians* Barnes and McDunnough), the Nantucket Pine Tip Moth (*Rhyacionia frustrana* (Comstock)), and the Ponderosa Pine Tip Moth (*Rhyacionia zozana* (Kearfott)) and a new host record of ascalaphid larvae (Neuroptera).

Hockeria is widely distributed throughout the Nearctic region (Fig. 53). The distribution map is based upon specimens examined by the author, and it encompasses most of the literature records. *Hockeria* are found in a variety of habitats and elevations. In California, some species (e.g. *eriensis* and *rubra*) range from coniferous forests to deserts. Several species range throughout the entire Nearctic region. A few species are known only from the western United States although additional collecting will likely extend their range. No species are restricted to the eastern United States or Mexico and interestingly, all Nearctic species have been collected in California. It is possible that the Nearctic species may also occur in the Palearctic or Neotropical regions; however, this awaits further study. Despite their broad range, *Hockeria* are rarely collected and uncommon in collections. Sweeping flowering vegetation or vegetation in general, and using Malaise-type traps and pan-traps are successful collecting techniques.

Many *Hockeria* specimens, representing seven species, were collected from a hydroelectric flume which runs through Foothill Woodland and Chamise Chaparral plant communities 660 m (2200 ft) in Tulare County, California. Large series of undescribed, rarely collected, and/or poorly represented species were collected from this

source (Halstead and Haines 1987). Without these specimens, species variation, male/female associations, and complete distributions would have been difficult to determine. During this study, somewhere between 1000 to 2000 specimens of *Hockeria* were examined.

Collections examined and museum acronyms are as follows: American Museum of Natural History, New York; Bernice P. Bishop Museum, Hawaii; California Academy of Sciences, San Francisco (CAS); California Department of Food and Agriculture, Sacramento (CDFA); California State University, Fresno; California State University, Sacramento; Canadian National Collection, Ottawa (CNC); Carnegie Museum of Natural History, Pittsburg, Pennsylvania (CMNH); Florida Department of Agriculture and Consumer Affairs, Gainesville (FDA); Fresno County Department of Agriculture Fresno, California; Illinois Natural History Survey, Champaign; Los Angeles County Museum of Natural History, California (LCM); Mississippi State University, Mississippi State; Natural History Museum of San Diego, California; Oregon Department of Agriculture, Salem; Royal Ontario Museum, Toronto (ROM); Texas A&M University, College Station; Tulare County Agricultural Commissioner's Office, Visalia, California; United States National Museum of Natural History, Washington D.C. (USNM); University of California, Berkeley; University of California, Davis; University of California, Riverside (UCR); University of Georgia, Athens (UOG); J. A. Halstead personal collection (JAH); H. A. Hespenheide personal collection, Los Angeles, California (HAH); R. B. Miller personal collection, Project City, California (RBM); R. D. Haines personal collection, Visalia, California (RDH).

Abbreviations include: T1 for tergite 1, etc.; OOL (ocular-ocellar line) for the smallest distance between the compound eye and lateral ocelli; OL (ocellar line) for the smallest distance between the anterior ocellus and lateral ocelli; LOD for lateral ocellar diameter; AOD for anterior ocellar diameter. All measurements were made in the flattest plane possible. Specimens were examined at 30 to 100×. A mylar, glare reducing screen was used in lighting specimens.

Key to Nearctic Species of *Hockeria*

1. Females; ovipositor present (Figs. 1–10) . . . 2
– Males; ovipositor absent . . . 10
2. Gaster (lateral view) about 1½× as long as wide, apex rounded (Figs. 8–10) . . . 3
– Gaster (lateral view) 2–3× as long as wide, apex pointed (Figs. 1–7) . . . 4
3. Hindfemur about 3× as long as wide, without ventral projections (Fig. 40, rarely as in Fig. 38); T1 punctate dorsally, with coriaceous band posteriorly . . . *eriensis* (Wallace)
– Hindfemur about 2× as long as wide, with an anterior toothlike projection and a rounded posterior projection (Fig. 39); T1 coriaceous . . . *bicolor* Halstead n. sp.
4. T1 punctate dorsally; forewing with a single clouded area under marginal vein (Figs. 45–46), rarely with no or 2 clouded areas; body black . . . 5
– T1 polished or slightly coriaceous dorsally; forewing with two clouded areas (Figs. 41–44) or a clear circular area laying within a large clouded area (Fig. 47); body partly or entirely red or orange . . . 6
5. Apex of ovipositor sheath with dorsal margin evenly rounded (lateral view) (Fig. 6); length about 3.8 mm . . . *burksi* Halstead n. sp.
– Apex of ovipositor sheath with dorsal margin angled (Fig. 5); length about 2.5 mm . . . *micra* Halstead n. sp.
6. Forewing with a clear circular area containing a dense patch of white setae, enclosed within a brown clouded area (Fig. 47) . . . *unipunctatipennis* (Girault)
– Forewing without a clear circular area (Figs. 41–44) . . . 7
7. Length less than 3 mm (2.5 to 2.8 mm) . . . 8
– Length greater than 4 mm (4 to 10 mm) . . . 9
8. Apex of ovipositor sheath with dorsal margin evenly rounded (lateral view) (Fig. 3); head, thorax, propodeum, and legs partly black . . . *hainesi* Halstead n. sp.
– Apex of ovipositor sheath with dorsal margin squared (Fig. 4); head, thorax, propodeum and legs orange . . . *brevipennis* Halstead n. sp.
9. Apex of ovipositor sheath with dorsal margin

evenly rounded (Fig. 2); head, thorax, propodeum, and legs partly black ..... *tenuicornis* (Girault)

– Apex of ovipositor sheath with dorsal margin angled (squared) (Fig. 1); head, thorax, propodeum and legs red to orange ..... *rubra* (Ashmead)

10. T1 punctate dorsally, posterior margin with a thin coriaceous band 11

– T1 coriaceous dorsally or if punctate, punctures extending ⅔ or less the length of T1; posterior margin with a broad coriaceous band. Or, if scutellum is strongly arched (Fig. 51) go to couplet 12 15

11. Wings darkly clouded throughout, commonly with an orangish tint; scape, tegulae, and legs usually orange; head (lateral view) oval and interantennal projection large (Fig. 27) ..... *unipunctatipennis* (Girault)

– Wings clear or with a small clouded spot; body color mostly black; head (lateral view) oblong and/or interantennal projection small (Figs. 25, 26, 30) 12

12. Scutellum strongly arched dorsally (Fig. 51); forewing with apical ⅔ clouded and a prominent brown spot under marginal vein ..... *eriensis* (Wallace)

– Scutellum slightly convex; forewing clear or with a faint clouded spot under marginal vein 13

13. Flagellomeres 2 to 2½× as long as wide; mesopleural acetabulum with sculpture between strong transverse carinae polished ..... *burksi* Halstead n. sp.

– Flagellomeres 3–8 1 to 1½× as long as wide; mesopleural acetabulum with sculpture between weak transverse carinae punctate 14

14. Propodeum with a strong longitudinal, submedian carina; anterior area of mesopleuron punctate and rugose ... *hainesi* Halstead n. sp.

– Propodeum with a oval reticulation of carinae medially; mesopleuron anteriorly smooth and polished, punctate only ventrally ..... *micra* Halstead n. sp.

15. T1 coriaceous dorsally; tergites without oval macropunctures; body partly or entirely orange to red-brown 16

– T1 punctate dorsally, sometimes punctures shallow and faint, appearing somewhat polished—if so, tergites with oval macropunctures (Fig. 52); body black 17

16. Scutellum with two, wide, triangular teeth at posterior margin, sculpture coriaceous centrally; head and thorax with well defined, moderately deep punctures which are separated by ½ to ⅓ their diameter, sculpture aciculate, polished; body orange to red and black ..... *bicolor* Halstead n. sp.

– Scutellum rounded at posterior margin, sculpture matte; head and thorax with shallow, vague punctures which are separated by ⅛ to ¼ their diameter, sculpture smooth, matte; body orange-brown .. *brevipennis* Halstead n. sp.

17. Posterior margin of scutellum with two triangular teeth; T1 dorsolaterally with macropunctures; band of macropunctures on other tergites prominent (Fig. 52) .. *rubra* (Ashmead)

– Posterior margin of scutellum rounded to truncate; T1 dorsolaterally without macropunctures, macropunctures on other tergites absent or faint and shallow ..... *tenuicornis* (Girault)

Hockeria eriensis (Wallace)

Figs. 8, 10, 18, 20, 28, 30, 38, 40, 48, 50, 51, 53

Stomatoceras rubra var. *eriensis* Wallace, 1942: 31, ♀ & ♂.

Stomatoceras rubrum eriense Wallace; Peck 1951: 585.

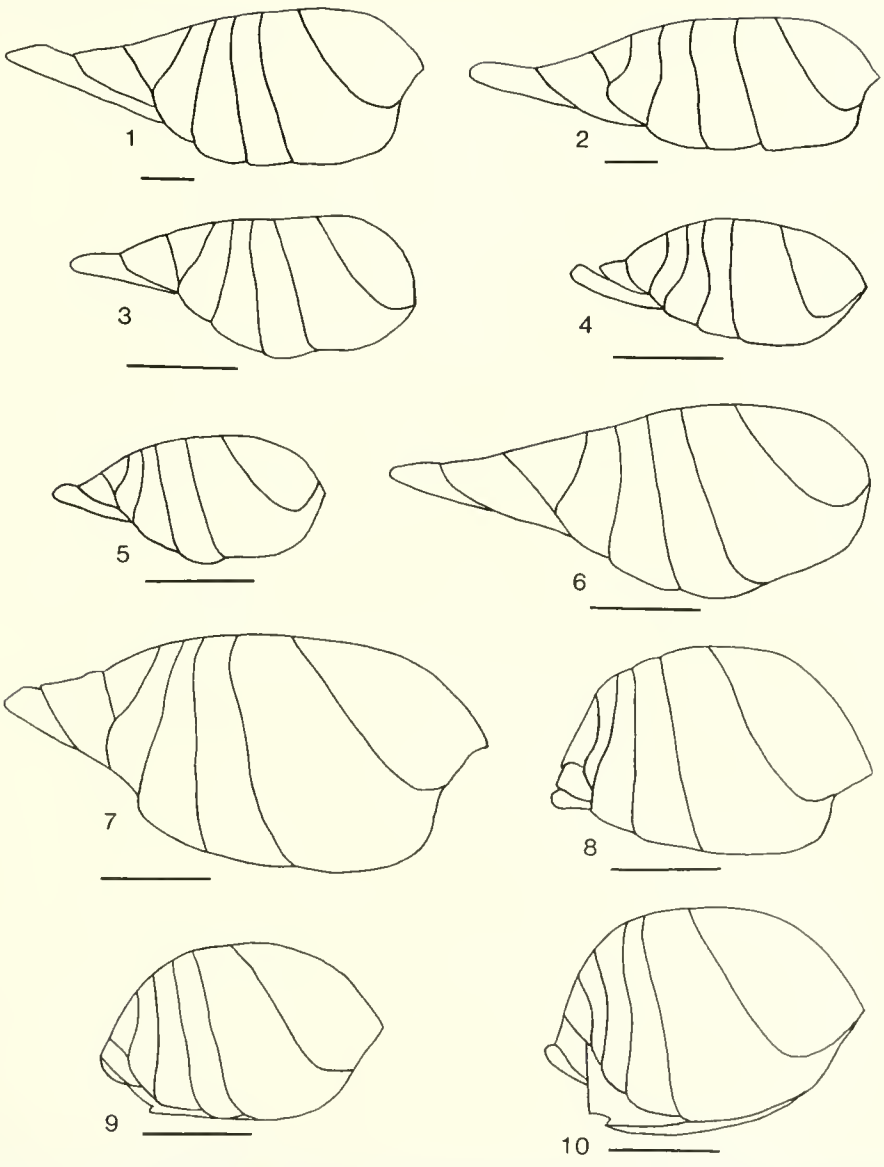
Hockeria eriensis (Wallace); Burks, in Steffan 1959: 304.

Female diagnosis (species).—Length about 5.0 mm. Red or orange with teeth of mandibles, mesosternum, anterior margin of mesoscutum, metanotum laterally, flagellomere 4 or 5 to apex, and teeth on ventral margin of hindfemur black.

Head as in Fig. 30. Antennae (Fig. 20) geniculate. Scutellum (Fig. 51) strongly arched. Forewing (Figs. 48, 50) with one or two clouded areas: at apex of marginal vein and in middle of wing near apex. Hindfemur (Fig. 40) narrow, elongate, without prominant ventral projections. Abdomen (Fig. 10) globose, apex blunt.

The female of *Hockeria eriensis* is most similar to *H. bicolor* n. sp. though is distinguished by its hindfemur shape. These two species (females) differ from other Nearctic *Hockeria* by having a narrow head, globose abdomen, and strongly arched scutellum.

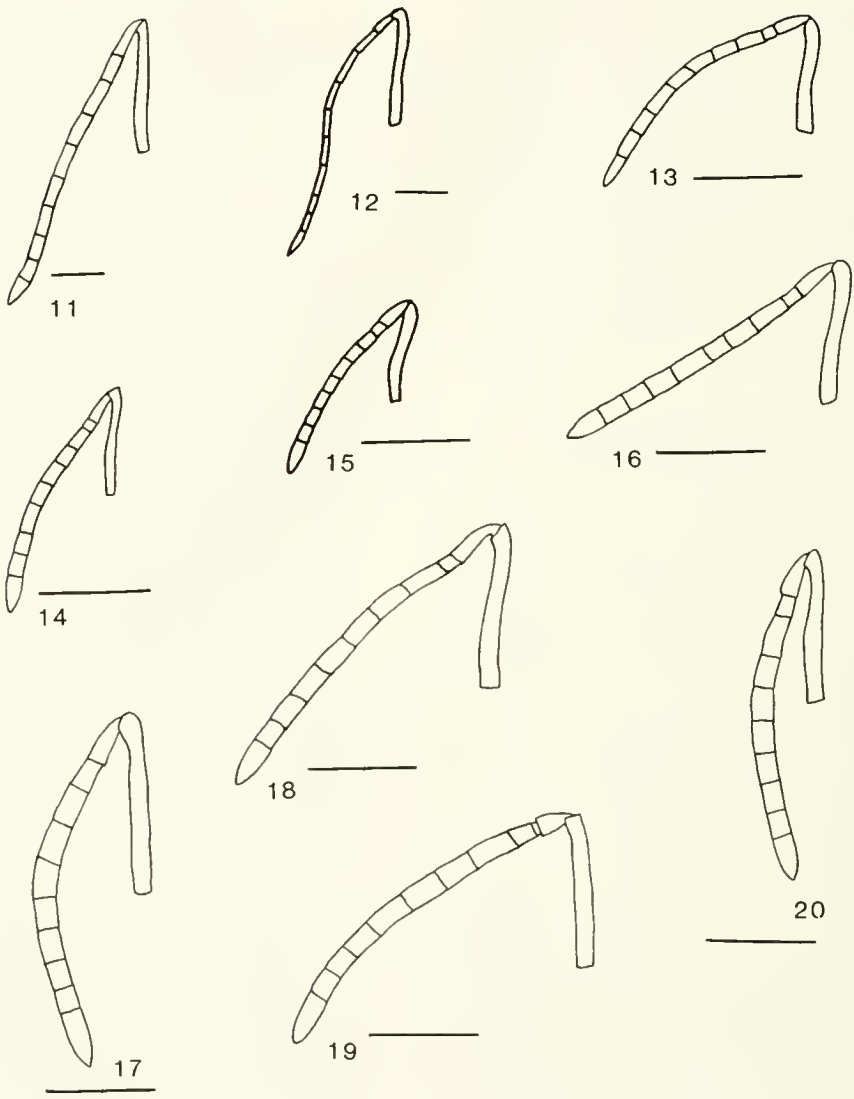
Variation (♀).—Length 2.5 to 5.0 mm. Most specimens are orange, or red with black areas. Wallace (1942) noted "dark females in which the head and thorax are almost entirely black, and the abdomen heavily



Figs. 1–10. *Hockeria* spp., abdomens of females (lateral view). 1, *rubra*. 2, *tenuicornis*. 3, *hainesi* n. sp. 4, *brevipennis* n. sp. 5, *micra* n. sp. 6, *burksi* n. sp. 7, *unipunctatipennis*. 8, *eriensis*, variation. 9, *bicolor* n. sp. 10, *eriensis*. Note differences in the overall shape and the shape of the ovipositor sheath. Scale lines 1.0 mm.

suffused with black." I have examined only a few dark colored specimens from the United States and the Dominican Republic. Forewing clouding varies from a single light colored spot to two dark spots. Forewing clouding of Dominican Republic specimens is unusually dark. Body morphology varies, including shape of antennae (Figs. 18, 20), head (Figs. 28, 30), abdomen (Figs. 8, 10), and hindfemora (Figs. 38, 40).

Male diagnosis (species).—Length about 4.9 mm. Black with tarsi and apices of tibiae orange. The strongly arched scutellum, two triangular teeth at its posterior margin, and



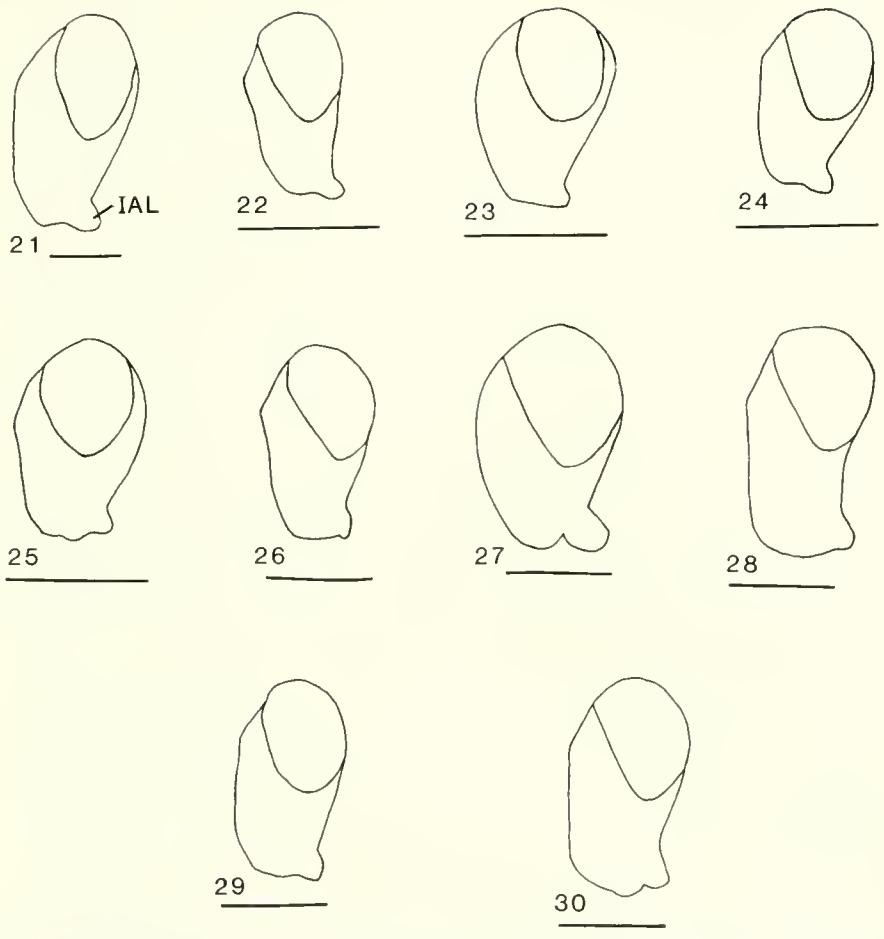
Figs. 11–20. *Hockeria* spp., antennae of females (lateral view). 11, *rubra*. 12, *tenuicornis*. 13, *hainesi* n. sp. 14, *brevipennis* n. sp. 15, *micra* n. sp. 16, *burksi* n. sp. 17, *unipunctatipennis*. 18, *eriensis*, variation. 19, *bicolor* n. sp. 20, *eriensis*. Note differences in the shape of the scape, pedicel, and flagellomeres. Scale lines 1.0 mm.

other characters presented in the key are distinguishing. This is the only previously described male in the Nearctic region.

Variation (♂).—Length 3.0 to 5.0 mm. The integument of T1 varies somewhat as indicated in the key. Scape and flagellum rarely red. Forewing clouding varies as in the female. Dominican Republic specimens with scape and legs (except trochanters) red-brown, and the two clouded areas of forewing dark.

Type material.—Paratypes in USNM examined. Holotype female and allotype male in CMNH. Type locality: Pennsylvania, Erie, Presque Isle. Paratypes in USNM and CMNH.

New distribution records.—MEXICO: Baja California Sur and Norte, Sonora, Mi-



Figs. 21–30. *Hockeria* spp., heads of females (lateral view). 21, *rubra*. 22, *tenuicornis*. 23, *hainesi* n. sp. 24, *brevipennis* n. sp. 25, *micra* n. sp. 26, *burksi* n. sp. 27, *unipunctatipennis*. 28, *eriensis*, variation. 29, *bicolor* n. sp. 30, *eriensis*. Note differences in the overall shape, size of the interantennal lobe (IAL), and slope of the face. Scale lines 1.0 mm.

choacan, Puebla, Oaxaca; VENEZUELA: Bolivar, Guarico, Aragua; GUATEMALA: Zacapa; DOMINICAN REPUBLIC: Pedernales, Independencia, Monte Cristi, and La Altagracia.

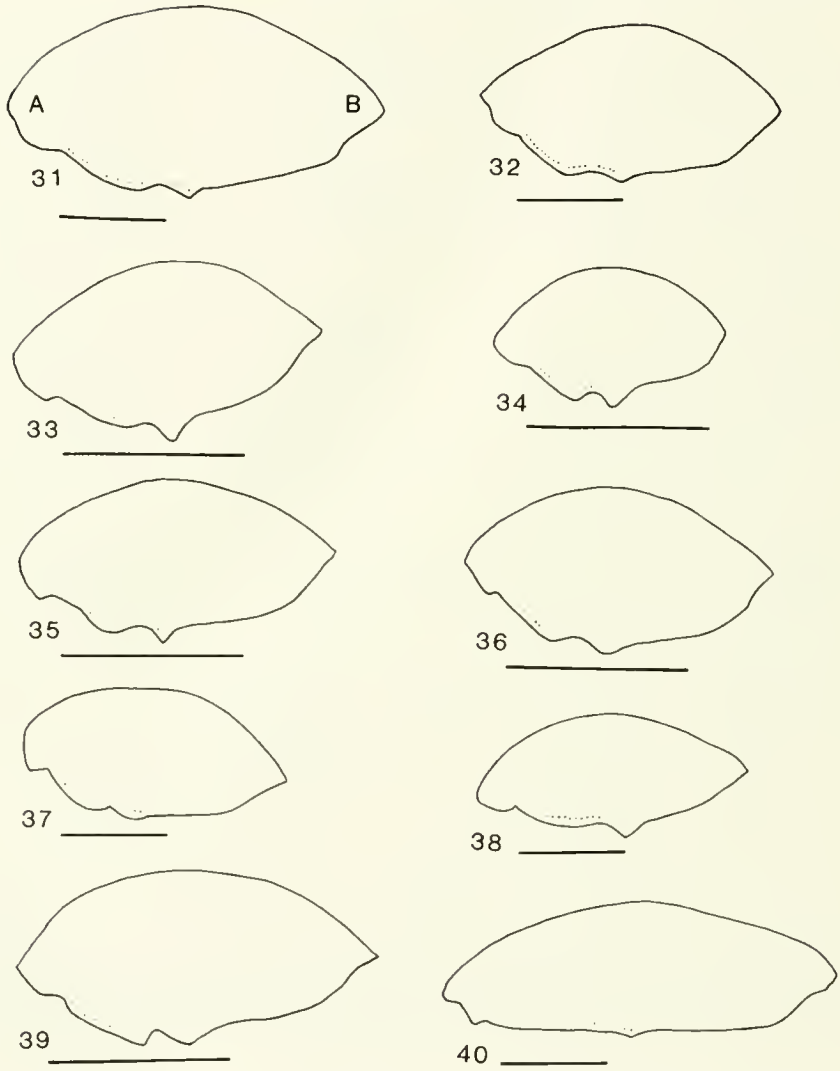
Flight period.—March to September.

Host.—*Myrmeleon* sp., *Myrmeleon immaculatus* DeGeer, *M. exitialis* Walker (2nd instar), *M. arizonicus* Banks, *Eremoleon* n.sp. in caves (Neuroptera: Myrmeleontidae).

Biology.—Wallace (1942) presented detailed information on the life history. *Hockeria eriensis* oviposits into and develops as an internal parasitoid of antlion larvae. The adult wasp emerges from the round, sand-covered antlion cocoon.

Floral records.—*Cleome serrulata* Pursh., *Gossypium hirsutum* L., *Larrea divaricata* Cav., *Baccharis, Croton,* and *Eriogonum.*

Comments.—The hindfemur of typical females (Fig. 40) is unlike that of any other Nearctic *Hockeria.* The structure may be related to its ovipositional behavior and host's defenses. Several chalcidids parasitize antlions (Steffan, 1959), and the shape

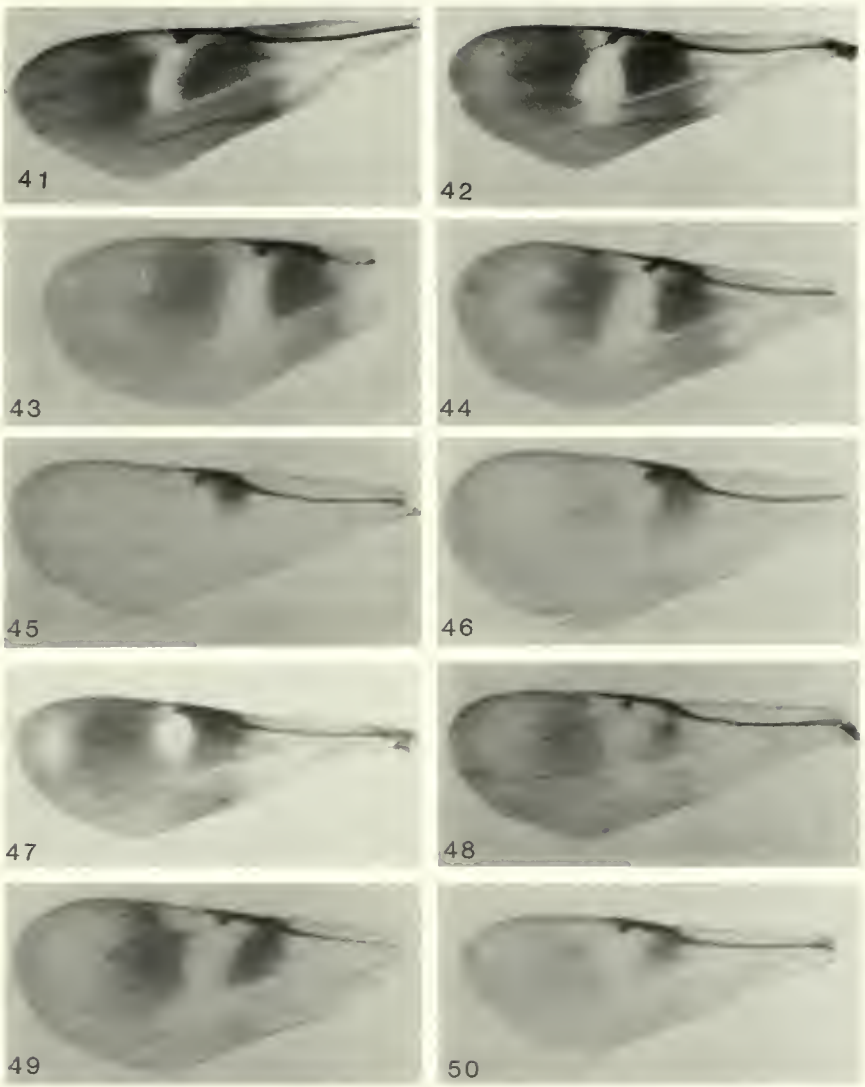


Figs. 31–40. *Hockeria* spp., hindfemora of females (lateral view), stipuling denotes area with teeth along ventral margin. Base (B) of femur to right, apex (A) to left. 31, *rubra*. 32, *tenuicornis*. 33, *hainesi* n. sp. 34, *brevipennis* n. sp. 35, *micra* n. sp. 36, *burksi* n. sp. 37, *unipunctatipennis*. 38, *eriensis*, variation. 39, *bicolor* n. sp. 40, *eriensis*. Note differences in the overall shape, and the location and size of the ventral projections. Scale lines 1.0 mm.

of the hindfemur among these species is variable.

Hockeria bicolor Halstead, New Species

Holotype female.—Length 3.1 mm. Black with scape, pedicel, annellus, interantennal lobe, flagellomeres 1, 2, clypeus, labrum, mandibles (except teeth), tegulae, submarginal vein of forewing, venation of hindwing, legs (except tarsal claws and teeth on ventral margin of hindfemur), ovipositor sheath (except apically), tergites ventrally, T1 along dorsoposterior margin, epipygidium, hypopygidium, and sternites orange; labial and maxillary palps, labium, remainder of venation, ventroposterior area of mesopleuron, small area on metapleuron an-

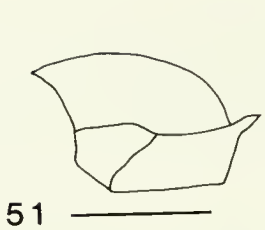


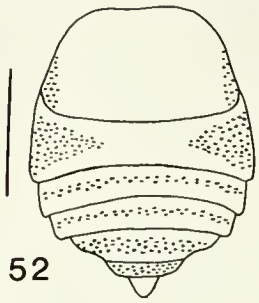
Figs. 41–50. *Hockeria* spp., forwings of females. 41, *rubra*. 42, *tenuicornis*. 43, *hainesi* n. sp. 44, *brevipennis* n. sp. 45, *micra* n. sp. 46, *burksi* n. sp. 47, *unipunctatipennis*. 48, *eriensis*, variation. 49, *bicolor* n. sp. 50, *eriensis*. Note differences in the number of clouded areas and the shape of hyaline areas.

terior to base of hindcoxae, and petiole orange-brown. Setae and pubesence silver.

Head (Fig. 29) narrow (lateral and dorsal view), polished, with umbilicate setigerous punctures; OOL < LO, OL = LO; antennae (Fig. 19) geniculate; interantennal lobe large; frons with anterior margin (lateral view) vertical; scrobe cavity slightly depressed, with strong transverse carinae, coriaceous; gena with shallow punctures; innerorbital ridge absent.

Thorax sculptured like head, integument aciculate; scutellum strongly arched, aciculation radiating from center, posterior margin with 2 small teeth; mesopleural acetabulum slightly depressed, transversely carinate, rugose; hindfemur (Fig. 39) ovoid, about 2× as long as high, ventral margin





Figs. 51, 52. 51, Scutellum, *Hockeria eriensis* male, lateral view. 52, Abdomen, *H. rubra* male, dorsal view; stipuling denotes macropunctures. Scale lines 1.0 mm.

with 2 projections and 23 small teeth; forewing (Fig. 49) reaching to apex of abdomen, with 2 clouded areas; hindwing clear.

Gaster (Fig. 9) equal in length to thorax, ovoid, dorsal margin convex (lateral view), apex blunt; T1 about ½ length of gaster, coriaceous (except for basolateral polished area); T2–6 finely coriaceous; T3–5 with a faint transverse line of shallow punctures, punctures on T6 pronounced and distributed throughout; T1–2 asetose (except for dorsolaterally), remainder of abdomen lightly setose; ovipositor not projecting posterior of abdomen.

Variation (♀).—Length 3.1 to 3.4 mm. Paratype from Florida with hindfemora brown. Paratypes from Trinidad and Brazil with tibiae (except apex), femora, tegulae, and abdomen brown to black.

Allotype male.—Length 3.3 mm. Black with scape, pedicel, labrum, clypeus, mandibles, trochanters, tibiae, and tarsi orange; coxae, femora, tegulae, and tergites ventrally orange-brown.

Head 1⅔× as high as wide (lateral view), 2½× as wide as long (dorsal view), triangular (frontal view), with setigerous umbilicate punctures, polished; scrobe cavity very shallow, almost flat, microridged and coriaceous; antennae geniculate, flagellum filiform; scape reaching dorsal margin of scrobe cavity, separated from anterior ocellus by AOD, coriaceous and setose (except for anterior margin); pedicel as wide as long, conical; flagellomere 1 2½× as long as wide, others 2× as long as wide; flagellum covered with dense, silver pilose; OOL ½ LOD, OL 1¼× AOD.

Thorax with shallow, widely spaced setigerous umbilicate punctures (separated by ⅓ to 1× their diameter), integument aciculate, prominent on pronotum and axillae; mesopleural acetabulum shallowly concave, integument transversely carinate and coriaceous; scutellum moderately convex, posterior margin with two wide, triangular teeth; hindfemur oval, 2× as long as high, a projection on ventral margin near middle, small teeth on ventral margin from projection to apex; legs coriaceous and setose; wings clear, with dark setae; postmarginal vein ½× marginal vein.

Gaster oval, slightly less than length of thorax; tergites densely coriaceous (except for polished band on anterior margin of T2–4); indications of faint transverse line of punctures on T3–6; T1 basolaterally with a patch of setae; T2–6 setose (except medially).

Variation (♂).—Length 3.2 to 3.5 mm. Two males (nontype) from Florida with hindfemora brown.

Type material.—Holotype ♀ (CAS No. 15241), U.S.A., CALIFORNIA, Tulare Co., Ash Mtn., Kaweah powerhouse #3, VIII-15-1982, from hydroelectric flume, R. D. Haines, D. J. Burdick, J. A. Halstead. Allotype ♂ (CAS No. 15241a). MISSOURI,

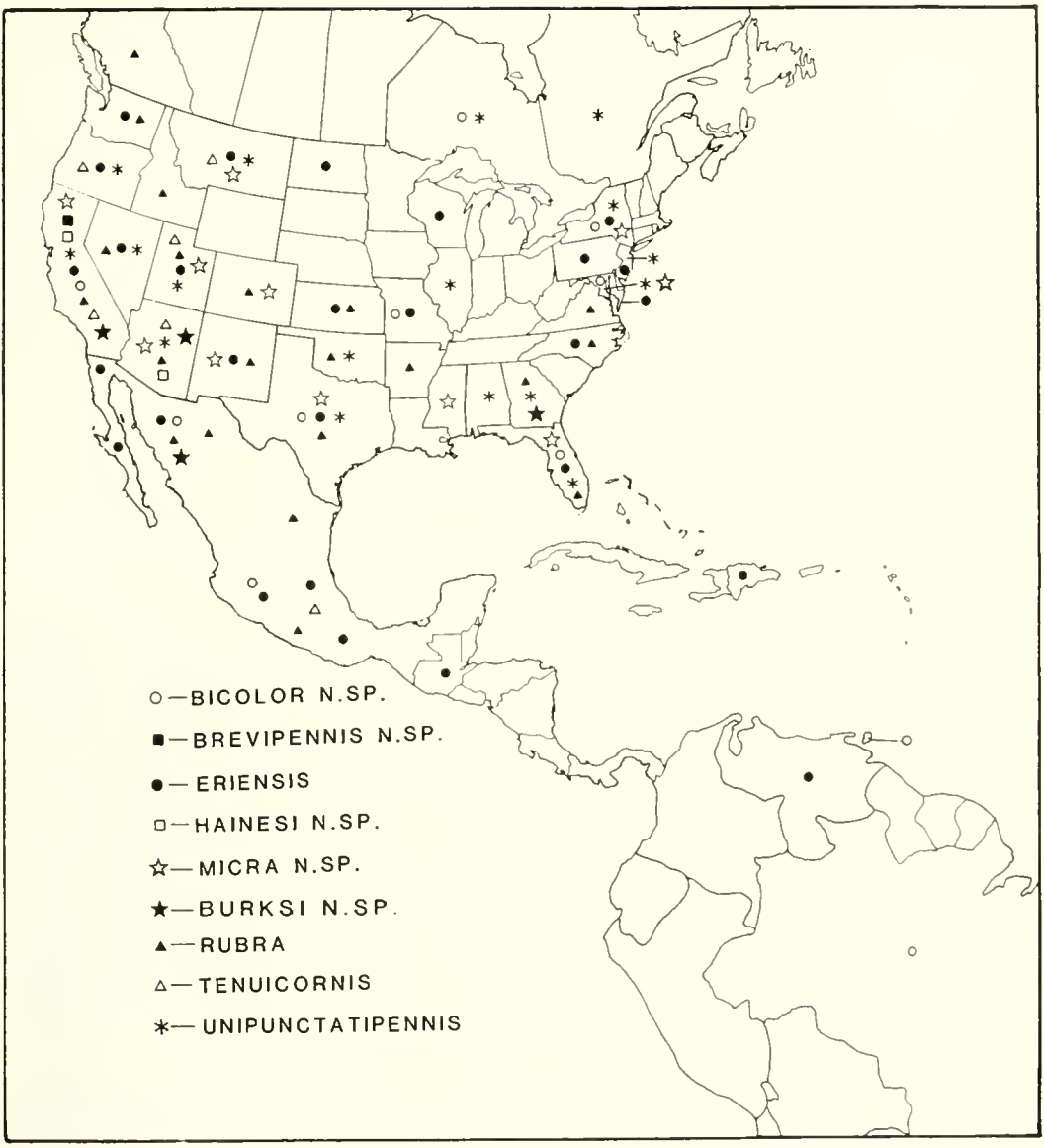


Fig. 53. Distribution of Nearctic species of *Hockeria*. The range of a couple species includes the Neotropical region. A symbol in a state, province, or country indicates the species is widely distributed in that region.

Boone Co., Columbia, V-16–31-1968, Malaise trap, F. D. Parker. Paratypes: CANADA, ONTARIO, 1♀, Lambton Co., Pinery Prov. Park, Riverside Cpgrnd., dry ground, open oak woodland, VII-1-1979, #770100, W. Maddison (ROM). U.S.A., CALIFORNIA, 15 ♀ with same data as holotype but collected VIII-27, 31-1982, VII-7, 17, IX-8, 18-1983, VI-23-1985, VI–VIII-1986 (CAS, USNM, JAH, RDH); 4 ♀, Madera Co., Bass Lake, VII-7-1986, R. D. Haines (RDH). TEXAS, 1 ♀, Uvalde Co., Uvalde, Speir Rch. 0.3 mi NW., V-7-1977, Malaise trap 9a-5p, T. Eichlin, M. Wasbauer (CDFA). MISSOURI, 2 ♀, Boone Co., Columbia, VII-16–31, VIII-16-1968, Malaise trap, F. D. Parker (USNM). MARYLAND, 14 ♀, Worc. Co., Shad Landing S. P., col.

IX-26-1986, em. XI-3-1986, G. L. Williams, ex. *Ululodes quadrimaculata* larvae in pupal cell (USNM). FLORIDA, 2 ♀, Alachua Co., Gainesville, S9-T10S-R18E, IV-16-1976, Malaise trap, W. H. Pierce (UCD). 1 ♀, Okaloosa Co., 4.5 mi N. Holt, Fla. A&M Res. Sta., Blackwater River State Forest, VI-17-1978, L. A. Stange (FDA). MEXICO, SONORA, 2 ♀, 7 mi S. Alamos, III-20-1985, R. B. Miller and L. Stange, 8 wasps emerged from one Guttipes group *Psammoleon* cocoon (RBM, CAS). JALISCO, 1 ♀, Puerto Vallarta, XII-5–10-1985, G. E. Bohart (USU). WEST INDIES, TRINIDAD, 2 ♀, Curepe Sta., Margarita, Circular Rd., I-28–II-9-1974, E. D. Bennett (CNC); 1 ♀, Tucker Valley I-20–26-1974, M. J. Sommeijer (CNC). BRAZIL, CAMPINAS, 1 ♀, Sp., Faz. Campininas, Mogi Guacu, I-1–8-1970, J. M. and B. A. Campbell (CNC).

Nontype material.—TEXAS, 2 ♂, as above. NEW YORK, 2 ♂, (AMNH). FLORIDA, 1 ♂, Marion Co., Ocala Natl. Forest, vic. Hopkins Prairie, V-11–18-1979, G. B. Fairchild, insect flight trap (FDA); 1 ♂, Monroe Co., Fleming Key, VII-16-1979, J. A. Acree and H. V. Weems, Jr., insect flight trap (FDA); 1 ♂, Highlands Co., Archbold Biol. Sta., IV-16–18-1982, L. L. Lampert, Malaise trap (FDA). MEXICO, SONORA, 2 ♂, as above.

Host.—*Psammoleon* sp. (Neuroptera: Myrmeleontidae); *Ululodes quadrimaculata* (Say) (Neuroptera: Ascalaphidae).

Comments.—The female of this species is most similar to *H. eriensis*. The characters in the key easily distinguish these two species. Refer to the *eriensis* female diagnosis section for additional comments.

Etymology.—The specific name, a Latin compound word, means two colors—referring to the red and black body coloration.

Hockeria unipunctatipennis (Girault)

Figs. 7, 17, 27, 37, 47, 53

Stomatoceras unipunctatipennis Girault, 1918: 127, ♀.

Stomatoceras unipunctatipennis unipunctatipennis Girault; Peck 1951: 585.

Hockeria unipunctatipennis unipunctatipennis (Girault); Peck 1963: 849.

Hockeria unipunctatipennis (Girault); Burks 1979: 862.

Stomatoceras unipunctatipennis americensis Girault, 1918: 127, ♀. **New Synonymy**

Stomatoceras unipunctatipennis americense Girault; Peck 1951: 585.

Hockeria unipunctatipennis americensis (Girault); Peck 1963: 849.

Hockeria americensis (Girault); Burks 1979: 861.

Female diagnosis (species).—Length about 5.0 mm. Black with mandibles (except teeth), scape, pedicel, flagellomeres 1, 2, pronotum, tegulae, coxae, tarsi, femora and tibiae of fore and middle leg, hindfemora (except centrally), apex of hindtibiae, mesopleuron (except centrally), metapleuron (except ventral margin), propodeum laterally, sternites, and ovipositor sheath (except apex) orange to red.

Head rounded, as in Fig. 27. Antennae (Fig. 17) geniculate. Scutellum slightly convex. Forewing (Fig. 47) clouded from apex of submarginal vein to near apex, with a circular white setose area under stigma. Hindfemur (Fig. 37) ovoid, with projections on ventral margin. Abdomen (Fig. 7) subaccuminate. T1 dorsally polished, lightly coriaceous laterally.

The contrasting black and orange body color, relatively long head (Fig. 27), and wing pattern easily distinguish *H. unipunctatipennis*. The relationship of *H. unipunctatipennis* to other Nearctic species of *Hockeria* is questionable.

Variation (♀).—Length 2.8 to 4.6 mm. Coloration is fairly uniform; however, I have examined three females from California and the holotype of *H. americensis* which have the thorax (except for the anterior margin of mesoscutum, axillae laterally, metanotum, propodeum, and legs) orange. Six females from Florida are completely red, the

largest specimens known (4.6 mm), and the circular spot in their forewing is slightly larger than usual.

Male description (pleisotype).—Length 3.4 mm. Black with mandibles, labrum, tegulae, and legs orange.

Head 1¼× as high as wide (lateral view), 2× as wide as long (dorsal view), triangular (frontal view), with dense setigerous umbilicate punctures, polished; frontogenal carina appearing as a ridge for ½ its length then as a suture to ventral margin of compound eye; scrobe cavity shallowly depressed, coriaceous; antennae geniculate, flagellum filiform; pedicel as wide as long, conical; flagellum with distinct flat, silver pilose; flagellomeres 2, 3 about 2½× as long as wide, flagellomeres 1 and 4–8 about 1½× as long as wide; scape reaching dorsal margin of scrobe cavity, separated from anterior ocellus by AOD, coriaceous and setose (except for anterior margin); OL 1½× AOD, OOL ½× LOD.

Thorax sculptured like head; scutellum as wide as long, slightly convex, posterior margin rounded; mesopleural acetabulum shallow, transversely carinate, polished; outer, dorsal side of hindcoxae aciculate dorsally, polished ventrally; hindfemur 2× as long as wide, a projection on ventral margin near middle, small teeth on ventral margin from projection to apex; legs coriaceous and setose; forewing and hindwing with an orangish tint, distinctly clouded, with dark setae and a darker spot under marginal vein of forewing.

Gaster slightly less than length of thorax; T1 ½ length of abdomen (dorsal view); T1 and anterior ½ of T2 punctate, remainder of tergites strongly coriaceous; T1 with patch of setae dorsolaterally, and laterally along posterior margin; remainder of tergites setose throughout (except for T2 medially).

Variation (♂).—Length 2.5 to 3.8 mm. Body rarely completely black.

Type material.—Holotype female in USNM examined. Type locality: West Virginia, Berkeley. Plesiotype male designated as such with red label and deposited in USNM; locality data: California, Tulare Co., Ash Mtn., Kaweah powerhouse #3. Holotype female of *H. americensis* (Girault) NEW SYNONYM in USNM examined. Type locality: New Jersey, Camden Co. This specimen differs only slightly in color from typical *H. unipunctatipennis*, and is therefore designated a junior synonym.

Host.—*Neodiprion excitans* Rohwer (Hymenoptera: Tenthredinidae).

New distribution records.—CANADA: Ontario and Quebec.

Flight period.—May to October.

Floral records.—*Eriogonum gracile, E. virgatum,* and *Sonchus oleraceous* L.

Hockeria rubra (Ashmead)

Figs. 1, 11, 21, 31, 41, 52, 53

Stomatoceras rubra Ashmead, 1894: 332, ♀.
Stomatoceras rubrum rubrum Ashmead; Peck 1951: 585.
Hockeria rubra (Ashmead); Burks, in Steffan 1959: 304.

Female diagnosis (species).—Length about 7.0 mm. Red or orange with teeth of mandibles, teeth on ventral margin of hindfemora, metanotum laterally, propodeum ventrally, and apical perimeter of ovipositor sheath black.

Head as in Fig. 21. Antennae (Fig. 11) geniculate. Scutellum slightly convex. Forewing (Fig. 41) clouded from near apex of submarginal vein to apex of wing, appearing as two separate clouded areas due to rectangular white setose area posterior to stigma. Hindfemur (Fig. 32) ovoid, with ventral projections. Abdomen (Fig. 1) elongate, accuminate. T1 polished, faintly coriaceous laterally. Apicodorsal margin of ovipositor sheath (Fig. 1) angled.

The female of *Hockeria rubra* is most similar to *H. tenuicornis* though is distinguished by its extensive red or orange body color, ovipositor shape, and clouded pattern of the forewing.

Variation (♀).—Length 4.0 to 10.0 mm. Rarely, specimens have the metanotum, tergites ventrally, epipygidium, and T5–6 black, the head rounded (lateral view) (as in Fig. 25), and the scutellum flat. Flagellomere 4 to apex of flagellum is occasionally black. A gynandromorph was described by Halstead (1988). Five atypical (color and morphology) females were found: lab produced, La Mesa, California (3 in USNM); Broken Bow, Oklahoma (INHS); and Monterrey, Mexico (CNC). These rare variants (except for the Oklahoma specimen) were reared from *Harrisina brillians* B. & McD. or *Harrisina* sp. (Lepidoptera: Zygaenidae). I was able to identify and associate the variant specimens in the USNM as *H. rubra* only because their parents were typical *H. rubra*. The variants from Oklahoma and Mexico are identical to the USNM variants. These variant specimens differ from typical *H. rubra* in the following characters: coloration black (except for red-brown apices of fore and middle femora, base and apices of tibiae, tarsi, tergites ventrally, and sternites posteriorly); flagellomeres slightly longer than wide; scape 10× as long as wide; head round, 1½× as tall as high (lateral view); scrobe cavity deeply concave, with prominent transverse carinae; thorax flat dorsally, especially scutellum; hindfemur broadly ovoid, 1¾× as long as wide; apex of ovipositor sheath with apicodorsal margin truncate; forewing clear; and body densely setose.

Male description (pleisotype).—Length 5.0 mm. Black with labrum, mandibles, apices of tibiae, tarsi, and T1–2 ventrally red-brown.

Head 2× as high as wide (lateral view), 2⅓× as wide as long (dorsal view), triangular (frontal view), with setigerous umbilicate punctures, lightly coriaceous; frontogenal carina appearing as a depressed line between base of mandible and ventral margin of eye; scrobe cavity depressed, dorsally microridged, ventrally coriaceous; antennae geniculate, flagellum robustly filiform; scape short, 7× as high as wide, not reaching anterior ocellus, lightly coriaceous; pedicel 2¼× as long as wide; flagellomeres 2× as long as wide, covered with short silver pilose; anterior ocellus at dorsal margin of scrobe cavity; OOL = LOD, OL 1⅓× AOD.

Thorax sculptured like head; scutellum aciculate, 1⅓× as long as wide, moderately convex, posterior margin with two rounded teeth; mesopleural acetabulum shallowly depressed, transversely carinate and polished; hindfemur oval, 2× as long as high, a small projection on ventral margin near middle, small teeth from projection to apex; hindcoxae with outer, dorsal side polished; legs aciculate and densely setose; wings clear, with dense dark setae; postmarginal vein ½× marginal vein.

Gaster oval (lateral view), length equal to thorax; T1 slightly less than ½ length of abdomen (dorsal view), basomedial area lightly punctate, basolaterally polished, remainder lightly coriaceous, a prominent patch of punctures and setae dorsolaterally; tergites lightly coriaceous (except for thin polished band on anterior margin of T2–5); T2–5 (except T2 medially) with a transverse band of macropunctures (Fig. 52); T6 punctate throughout; tergites setose (except for T2 medially and T1 as noted above).

Variation (♂).—Length 3.0 to 6.0 mm. Flagellum rarely red.

Type material.—Holotype female in USNM examined. Type locality: Texas. Paratypes in USNM and AMNH. Plesiotype male designated as such with red label and deposited in USNM; locality data: California, Tulare Co., Ash Mtn., Kaweah powerhouse #3.

New distribution records.—CANADA: British Columbia; U.S.A: Washington, Idaho, Nevada, Utah, Colorado, New Mexico, Georgia, and North Carolina; MEXICO: Chihuahua, and Monterrey.

Flight period.—May to October.

Host.—*Harrisina brillians* (Lepidoptera: Zygaenidae).

Floral records.—*Acacia Greggii* Gray,

Chrysothamnus nauseosus (Pall.), *Eriogonum virgatum* Benth., *Gossypium hirsutum, Stanleya pinnata* (Pursh), *Yucca elata* (Engelm.), *Eriogonum,* and *Prosopis.*

Comments.—*Harrisina brillians* (Western Grapeleaf Skeletonizer) larvae defoliate grapes (*Vitis* spp.) and two ornamental vines, Virginia Creeper (*Parthenocissus tricuspidata* (Sieb. & Zucc.)) and Boston Ivy (*P. quinquefolia* (L.)) in the southwestern United States and Mexico (Stern 1981). In 1952 and 1953, low numbers (45 and 35, respectively) of *H. rubra* were released into California (San Diego area) to control the skeletonizer (Clausen 1955; 1956), despite *H. rubra* being native to California.

From 1977 to 1983 Biological Control Services Program personnel, CDFA (including author 1981–1983) reared approximately 200,000 skeletonizer larvae and/or pupae from several locations in California, but no specimens of *H. rubra* were reared. This indicates that *H. rubra* has little impact upon *Harrisina brillians* populations in California.

Hockeria tenuicornis (Girault)

Figs. 2, 12, 22, 32, 42, 53

Stomatoceras tenuicornis Girault, 1918: 127, ♀.

Stomatoceras tenuicorne Girault; Peck 1951: 585.

Hockeria tenuicornis (Girault); Peck 1963: 849.

Female diagnosis (species).—Length about 7.0 mm. Orange with teeth of mandibles, inneroccular area, mesosternum, pronotum anteriorly, mesoscutum medially, lateral corner of axillae, scutellum medially, metanotum, propodeum, hindtibiae anteriorly, apex of ovipositor sheath, abdomen (except ventrally), and hindfemora centrally black.

Head as in Fig. 22. Antennae (Fig. 12) geniculate. Scutellum slightly convex. Forewing (Fig. 42) like *rubra* except white setose area elliptical. Hindfemur (Fig. 32) ovoid, with ventral projections. Abdomen (Fig. 2) elongate, accuminate. T1 polished, coriaceous laterally and dorsoposteriorly. Apicodorsal margin of ovipositor sheath (Fig. 2) evenly rounded.

The female of *Hockeria tenuicornis* is most similar to *H. rubra* though is distinguished by its black and orange body color, ovipositor shape, and clouded pattern of the forewing.

Variation (♀).—Length 3.5 to 7.0 mm. Dark specimens with scape, flagellomere 2 to apex, entire thorax dorsally, occiput, scrobe cavity, hindtibia, and hindfemur black; light colored specimens with pronotum, scutellum, T1–2 laterally, and hindfemur orange.

Male description (pleisotype).—Length 4.3 mm. Black with mandibles, labrum, trochanters, apices of femora, outerside of middle femora, apices of tibiae, tarsi, and T1–2 ventrally orange.

Like *H. rubra* male except for the following characters: body coloration and length, frontogenal carina a ridge extending ½ way to ventral margin of compound eye; scutellum only slightly longer than wide, posterior margin without teeth, evenly rounded; T1 densely punctate medially in basal ⅔, polished only near base, without prominent punctures dorsolaterally; tergites densely coriaceous (except for aciculate band on anterior margin of T2–5); band of macropunctures on T2–5 faint; punctures on T6 obscured by coriaceous sculpture; outer, dorsal side of hindcoxae mostly aciculate.

Variation (♂).—Length 3.0 to 5.0 mm. Flagellum rarely red.

Type material.—Holotype female in USNM examined. Type locality: Arizona, Santa Rita Mtns. Plesiotype male designated as such with red label and deposited in USNM; locality data: California, Tulare Co., Ash Mtn., Kaweah powerhouse #3.

New distribution records.—U.S.A.: Oregon and Utah; MEXICO: Tlaxcala.

Flight Period.—May to October.

Host.—*Rhyacionia zozana* (Kearfott)

(Lepidoptera: Tortricidae) larvae and possibly pupae (Halstead and Niwa 1987).

Floral records.—*Adenostoma fasciculatum* H. & A., *Eriogonum fasciculatum* Benth., *E. gracile* Benth., *E. inflatum* Torr. & Frem., *Astragalus lentiginosus* Dougl., *Euphorbia,* and *Salvia.*

Hockeria hainesi Halstead, New Species

Figs. 3, 13, 23, 33, 43, 53

Holotype female.—Length 2.8 mm. Orange with flagellum (except for flagellomere 1), ocellar area, teeth of mandibles, mesosternum, anterior and posterior margins of scutum, submedial corner of scapula, axillae, metanotum, scutellum laterally, propodeum basally, ventral margin of metapleuron, T1 sublaterally, T3–6, T2 dorsally, epipygidium, ovipositor sheath, basal ½ of tibiae, tarsal claws, and teeth on ventral margin of hindfemur black; T1 (except sublaterally), T2 laterally, scutum (except for anterior and posterior margins), and scutellum (except laterally) dark orange-brown. Setae and pubesence silver.

Head (Fig. 23) rounded (lateral view), with shallow umbilicate setigerous punctures, polished; OOL ½ LOD, OL < AOD; antennae (Fig. 13) geniculate; interantennal lobe rounded; frons with anterior margin (lateral view) sloped; scrobe cavity slightly depressed, coriaceous; gena with shallow punctures; innerorbital ridge absent.

Thorax sculptured like head, flat dorsally; scutellum slightly convex, posterior margin with two broad teeth; mesopleural acetabulum with strong transverse carinae, sculpture rugose; hindfemur (Fig. 33) ovoid, about 2× as long as high, ventral margin with 2 projections and 21 small teeth; forewing (Fig. 43) with apex reaching to near apex of abdomen, with two clouded areas; hindwing clear.

Gaster (Fig. 3) shorter than head and thorax together, elongate, apex pointed, dorsal margin flat (lateral view); tergites strongly coriaceous (except for smooth band along posterior margins and basal ½ of T1); ovipositor sheath with apicodorsal margin evenly rounded; tergites (T1 laterally and T2 except medially) setose; ovipositor projecting posterior of abdomen.

Variation (♀).—Length 2.5 to 2.8 mm. Two paratypes with occiput medially, posterior of ocellar area orange-brown.

Allotype male.—Length 3.0 mm. Black with mandibles, apex of femora and tibiae, and tarsi orange; pedicel and flagellum brown.

Like *H. micra* male except for color, propodeal, and mesopleural characters presented in the key (couplet 14).

Variation (♂).—Known only from allotype.

Type material.—Holotype ♀ (CAS No. 15243), U.S.A., CALIFORNIA, Tulare Co., Ash Mtn., Kaweah powerhouse #3, IX-8-1983, from hydroelectric flume, J. A. Halstead, R. D. Haines, D. J. Burdick. Allotype ♂ (CAS No. 15243a), ARIZONA, Cochise Co., Chiricahua Mts., S.W.R.S. 5400′, VII-31-1980, V. Roth. Paratypes: 6 ♀ paratypes with same data as holotype but 5 collected: X-1-1982, VII-3-1983, IX-2, 15-1984, VII-12-1986 (CAS, USNM, JAH, RDH). ARIZONA, 2 ♀, Cochise Co., Chiricahua Mts., S.W.R.S. 5400′, VI-29-1980, V-4–7-1980, V. Roth (CNC).

Host.—Unknown.

Comments.—The female of this species is most similar to *H. tenuicornis. Hockeria hainesi* resembles a minute specimen of *H. tenuicornis* though is distinguished by its rounded head and small body size.

Etymology.—The specific name, a noun in the genitive case from a modern personal name, is in honor of R. D. Haines—a friend who collected most of the specimens.

Hockeria brevipennis Halstead, New Species

Figs. 4, 14, 24, 34, 44, 53

Holotype female.—Length 2.6 mm. Orange with flagellum (except flagellomere 1), teeth of mandibles, apex of ovipositor

sheath, teeth on ventral margin of hindfemur, and tarsal claws black; marginal and postmarginal veins of forewing, apex of submarginal vein of hindwing, and T3–6 (except ventrally) orange-brown. Setae and pubesence silver.

Head (Fig. 24) rounded (lateral view), with shallow umbilicate setigerous punctures, individual punctures difficult to distinguish, polished, setation sparse and short; OOL ⅓ LOD, OL = AOD; antennae (Fig. 14) geniculate; interantennal lobe rounded; frons with anterior margin (lateral view) sloped; scrobe cavity slightly depressed, faintly coriaceous; gena glabrous; innerorbital ridge absent.

Thorax sculptured like head, flat dorsally; scutellum slightly convex, posterior margin rounded, with 2 vague rounded teeth; mesopleural acetabulum weakly depressed, coriaceous, with a few vague transverse carinae; hindfemur (Fig. 34) ovoid, about 2× as long as high, ventral margin with 2 projections and 21 small teeth; forewing (Fig. 44) short, apex reaching to middle of abdomen, with two clouded areas; hindwing clear.

Gaster (Fig. 4) slightly longer than head and thorax together, subelongate, dorsal margin flat (lateral view), apex subacuminate; T1 polished dorsally, coriaceous laterally, basolaterally with a patch of setae; T2–6 coriaceous, sparsely setose, setae more prominent sublaterally; ovipositor projecting slightly posterior of abdomen.

Variation (♀).—Length 2.6 to 2.8 mm. One paratype with metanotum dark orange-brown. Two paratypes with T3–6 completely orange.

Allotype male.—Length 2.3 mm. Orange with head, thorax (dorsally), and scape orange-brown.

Like *H. bicolor* male except for the following: OL 2¼× AOD; scrobe cavity coriaceous; flagellomere 1 2× as long as wide; head and thorax with shallow, vaguely defined punctures, rugose, matte; scutellum with posterior margin rounded; mesopleural acetabulum with a few vague, transverse carinae, rugose.

Variation (♂).—Known only from allotype.

Type material.—Holotype ♀ (CAS No. 15242) and Allotype (CAS No. 15242a), U.S.A., CALIFORNIA, Riverside Co., Menifee Valley (hills on west end), 33°39′N, 117°13′W, 1800 ft. elevation, pan trap under *Eriogonum gracile*, X-17–22-1981, J. D. Pinto. Paratypes: 4 ♀ with same data as holotype except collected IX-16–22-1981 in pan trap under *Eriogonum*, and VIII-18–29-1982 in pan trap under *E. fasciculatum* (CAS, UCR, USNM, JAH).

Host.—Unknown.

Comments.—The female of this species is most similar to *H. micra* n. sp. but, *brevipennis*'s orange body color and T1 polished dorsally are distinguishing.

Etymology.—The specific name, a Latin compound word, means short wings—calling attention to the wings of this species.

Hockeria micra Halstead, New Species

Figs. 5, 15, 25, 35, 45, 53

Holotype female.—Length 2.5 mm. Black with basal ⅓ of scape, annellus, flagellomere 1, mandibles (except teeth), palps, middle coxae, apical ¼ and base of hindcoxae, trochanters, apex and base of femora, apex of tibiae, tarsi (except claws), tegulae, hypopygidium, and petiole ventrally orange. Setae and pubesence silver.

Head (Fig. 25) rounded (lateral view), with shallow umbilicate setigerous punctures, polished; OOL ½ LOD, OL < AOD; antennae (Fig. 15) geniculate; interantennal lobe rounded; frons with anterior margin (lateral view) sloped; scrobe cavity slightly depressed, coriaceous; gena rugose; innerorbital ridge absent.

Thorax sculptured like head, flat dorsally; scutellum slightly convex, posterior margin with two broad teeth; mesopleural acetabulum with vague transverse carinae, coriaceous; hindfemur (Fig. 35) ovoid, about 2×

as long as high, ventral margin with 2 projections and 21 small teeth; forewing (Fig. 45) with apex extending to apex of abdomen, with a single clouded area under marginal vein; hindwing clear.

Gaster (Fig. 5) as long as head and thorax together, subaccuminate, apex pointed, dorsal margin flat (lateral view); ovipositor sheath with apicodorsal margin angled (squared); tergites strongly coriaceous (except for smooth band along posterior margins and basal ½ of T1); tergites (T1 laterally and T2 except medially) setose; ovipositor projecting posterior of abdomen.

Variation (♀).—Length 2.0 to 2.5 mm. Commonly, orange areas are brown or black. Commonly, scape orange basally and brown apically, rarely entire scape black. Flagellomere 1 rarely brown or black. Flagellomere 2 occasionally orange. One paratype with ventral ½ of T1–2 orange-brown. Two paratypes with fore and middle coxae orange. Four paratypes with tegula black. Six paratypes (Maryland and Florida, Lee Co.) with two clouded areas in forewing. Basal clouded area larger and darker than in holotype; distal area small and oval, located in middle of wing near apex. One paratype (Ivanpah) with forewing clear.

Allotype male.—Length 2.1 mm. Black with mandibles, apices of femora and tibiae, and tarsi orange.

Like *H. burksi* n. sp. male except for the following: head 1⅓× as high as wide (lateral view); flagellomeres 3–8 1⅓× as long as wide; scrobe cavity coriaceous; mesopleural acetabulum with a few vague transverse carinae, punctate; posterior margin of scutellum appearing rounded, with two vague broad teeth; forewing with spot under marginal vein vague; postmarginal vein 1¼× marginal vein. Propodeum in medial area a reticulation of oval carinae. Anterior area of mesopleuron smooth and polished, punctate only in basal ⅓.

Variation (♂).—Length 1.8 to 2.3 mm. Forewing rarely hyaline.

Type material.—Holotype ♀ (CAS No. 15244) and Allotype ♂ (CAS No. 15244a), U.S.A., CALIFORNIA, Tulare Co., Ash Mtn., Kaweah powerhouse #3, X-5-1982, from hydroelectric flume, J. A. Halstead, D. J. Burdick, R. D. Haines. Paratypes: CALIFORNIA, 34 ♀ paratypes with same data as holotype except collected VI–IX 1982 to 1986 (CAS, USNM, CIS, UCR, AMNH, UCD, CNC, JAH, RDH, HAH). 1 ♀, Kern Co., Shafter, VIII-2-1955, J. Powell (CIS). 1 ♀, Alameda Co., Livermore 10 mi E., Tesla Rd., VIII-9-1959, G. I. Stange (CAS). 1 ♀, Stanislaus Co., Del Puerto Cyn., VIII-7-1978, N. J. Smith (UCD). 1 ♀, San Bernardino Co., Ivanpah, 12 mi SE., V-1-1956, P. D. Hurd (CIS). 1 ♀, Marin Co., Novato, X-13-1968, in swimming pool, I. Baker (CDFA). 31 ♀, Fresno Co., Panoche Road at San Benito Co. line, VIII-11-1982, IX-9-1982, VIII-24-1983, on *Euphorbia* mats, J. A. Halstead, N. J. Smith (CAS, USNM, FCDA). 6 ♀, Riverside Co., Menifee Valley (hills on west end), 33°39′N, 117°13′W, 1800′ elevation, V-24–VI-2-1982, IX-16–21-1981, VI-13–18-1981, pan traps under *Adenostoma fasciculatum* and *Eriogonum* (UCR); 5 ♀, Indio, T5S, R7E, S14, XI-3-1983, insectary reared from *Coleophora klimeschiella* on *Salsola iberica*, R. D. Goeden and D. W. Ricker (UCR). MONTANA, 1 ♀, Missoula, VIII-7-1950, B. Malkin (CAS). COLORADO, 1 ♀, Gunnison Co., Black Mesa, 10.7 mi W. Sapinero, VIII-19-1966, T. C. Emmel (LCM). 1 ♀, Dolores Co., 21 mi NE. Delores, Cottonwood Spring (Montezuma Co.), 7800′, VII-23-1976, N. L. Herman (AMNH). ARIZONA, 3 ♀, Cochise Co., 5 mi NNW. Portal, San Simon Road, 4600′, 31°59′N, 109°10′W, V-18-1985, flowers of *Chamaesyce*, H. A. Hespenheide (HAH); 1 ♀, 2 mi ESE. Portal, VI-7-1979, at mesquite, H. A. Hespenheide (HAH). NEW MEXICO, 1 ♀, Hidalgo Co., 6 mi N. Rodeo, Antelope Corral, 4040′, 31°55–56′N, 109°00–01′W, V-22-1985, H. A. Hespenheide (HAH). MISSISSIPPI, 1 ♀, Agr. Coll. Miss. VIII-31-1911, Pecan, E. C. Crockett (MSU). MARYLAND, 2 ♀, Worc. Co., Snow

Hill, IX-13-1973, *Rhyacionia frustrana* (USNM). FLORIDA, 1 ♀, Highlands Co., Archbold Biol. Sta., IV-22–25-1982, L. L. Lampert, Jr. and H. V. Weems, Jr., insect flight trap (FDA). 4 ♀, Lee Co., Lehigh Acres, IV-6-1988, exit cocoons of *Phormoestes palmettovora* Heppner, VII-2–14-1988, J. R. Brushwein (USNM, FDA).

Nontype material.—CALIFORNIA, 3 ♂, Riverside Co., Riverside, on *Lotus, Eriogonum auriculatum, E. gracile,* X-15-1925, Timberlake (UCR); 1 ♂, 18 mi W. Blythe, III-31-1978, N. J. Smith (UCD); 1♂, San Timoteo Cyn., Malaise trap, 10 am to 3 pm, IX-9-1974, M. Wasbauer and R. McMastear (CDFA); 5 ♂, Indio—as above. 1 ♂, San Bernardino Co., 5 mi N. Renoville, Salt Crk., *Atriplex hymenelytra,* IV-17-1974, F. G. Andrews (CDFA); 1 ♂, Mill Crk., *Eriogonum gracile,* X-1-1951, Timberlake (UCR); 1 ♂, Needles, V-3-1964, G. E. Bohart (USU); 1 ♂, San Lucas, V-20-1935, Timberlake; 1 ♂, 12 mi SE. Ivanpah—as above. 2 ♂, Marin Co., Novata—as above. 1 ♂, San Diego Co., Warner Sprgs., Agua Calicate Crk., 3100′, VIII-23/25-1980, Malaise trap, M. Wasbauer and P. Adams (CDFA). 1 ♂, Placer Co., 4 mi S. Rocklin, V-26-1979, Malaise trap, M. Wasbauer and P. Adams (CDFA). 1 ♂, Stanislaus Co., Del Puerto Cyn.—as above. 1 ♂, Humbolt Co., Redwood Crk., Redwood Vly., N. of Hyw. 299, 650′, VIII-10-1968, H. B. Leech (CAS). 1 ♂, Kern Co., Shafter—as above. 1 ♂, Fresno Co., S. of Coalinga, Warthan Cyn. Rd., S36, T20S, R12E, I-19-1981, N. J. Smith (FCA-CO). 30 ♂, Tulare Co., Ash Mtn. Kaweah powerhouse #3—as above (CAS, RDH, JAH). 1 ♂, Nevada Co., Boca, VII-23-1970, E. E. Grissell, Great Basin Desert (FDA). ARIZONA, 1 ♂, 5 mi W. Manicopa Aguila, VI-22-1971, G. Bohart and P. Torchio (USU). UTAH, 1 ♂, St. George, VI-13-1930, E. Davis, *Gutierrezia lucida* (USNM). TEXAS, 1 ♂, Uvalde Co., 3 mi NW. Uvalde, Speir Rch., V-4-1977, T. Eichlin and M. Wasbauer (CDFA). NEW YORK, 2 ♂, New York (AMNH). FLORIDA, 2 ♂, Lee Co.—as above.

Host.—*Rhyacionia frustrana* (Lepidoptera: Tortricidae); *Coleophora klimeschiella* Toll (Lepidoptera: Coleophoridae) (Goeden et al. 1987); and *Phormoestes palmettovora* (Lepidoptera: Choreutidae) (Brushwein, in prep.). *Rhyacionia* are pests of pine trees (*Pinus* spp.). *Coleophora klimeschiella,* a biological control agent against Russian thistle (*Salsola australis* R. Brown), was released into the United States (California) in 1977 (Goeden et al. 1987).

Comments.—The female of this species is most similar to *H. burksi* n. sp. but, *micra* is smaller in length and the ovipositor has the dorsal margin angled.

Etymology.—The specific name, a Latinized Greek adjective, means small—referring to the size of this species.

Hockeria burksi Halstead, New Species

Figs. 6, 16, 26, 36, 46, 53

Holotype female.—Length 3.8 mm. Black with base of scape, tegulae, coxae (except basal ⅔ of hindcoxae), trochanters, fore and middle femora basally, hindfemur (except base and dorsal edge), fore and middle tibiae apically, hindtibiae, submarginal vein of forewing, venation of hindwing, tarsi (except claws), and ovipositor sheath orange; labrum, mandibles (except teeth), hypopygidium, annellus, flagellomere 1, palps, and remainder of forewing venation orange-brown. Setae and pubscence silver.

Head (Fig. 26) rounded (lateral view), polished, with dense umbilicate setigerous punctures; OOL ½ LOD, OL < AOD; antennae (Fig. 16) filiform; interantennal lobe rounded; frons with anterior margin (lateral view) sloped; scrobe cavity slightly depressed, coriaceous; innerorbital ridge absent.

Thorax sculptured like head; scutellum low, gently convex, posterior margin with two broad teeth; mesopleural acetabulum with strong transverse carinae, coriaceous;

hindfemur (Fig. 36) ovoid, about 2× as long as high, ventral margin with 2 projections and 21 small teeth; forewing (Fig. 46) with apex reaching to base of epipygidium, with a single clouded area under marginal vein; hindwing clear.

Gaster (Fig. 6) shorter than head and thorax together, elongate, apex pointed, dorsal margin flat (lateral view); tergites strongly coriaceous (except for smooth band along posterior margins and basal ½ of T1); ovipositor sheath with apicodorsal margin evenly rounded; tergites (T1 laterally and 72 except medially) setose; ovipositor projecting posterior of abdomen.

Variation (♀).—Length 3.5 to 3.9 mm. Black or orange-brown areas in holotype commonly brown or orange, respectively. One paratype (Riverside) with T1–5 ventrally, scape, pedicel, flagellomeres 1–2, sternites, hypopygidium, and legs orange. One paratype (San Diego Co.) with two clouded areas in forewing: under marginal vein and in middle near apex.

Allotype male.—Length 3.5 mm. Black with tibiae and tarsi apically orange-brown.

Head 1¼× as high as wide (lateral view), 2⅓× as long as wide (dorsal view), triangular (frontal view), with umbilicate setigerous punctures, polished; frontogenal carina a prominant ridge in ventral ½, remainder reduced, extending from base of mandible to ventral margin of compound eye; scrobe cavity shallowly depressed, ventrally coriaceous, dorsally transversely microridged; antennae filiform; scape reaching dorsal margin of scrobe cavity, separated from anterior ocellus by AOD, coriaceous and setose except for anterior margin; pedicel as wide as long, conical; flagellomeres 1 and 2 2½× as long as wide, others 2⅕× as long as wide; OL 1× AOD, OOL ½× LOD.

Thorax sculptured like head; mesopleural acetabulum shallow, transversely carinate, polished; scutellum as wide as long, moderately convex, anterior margin with two broad teeth; axillae and pronotum coriaceous laterally, remainder of thorax faintly aciculate; outer, dorsal side of hindcoxae coriaceous; hindfemur oval, 2× as long as high, ventral margin evenly rounded, without a large projection or tooth, small teeth on ventral margin from middle to apex; legs coriaceous and setose; forewing with a clouded spot under marginal vein, with dark setae; postmarginal vein equal to marginal vein.

Gaster oval (lateral view), equal in length to head and thorax together; T1 about ½× gaster (dorsal view), punctate, a thin coriaceous band along posterior margin, densely coriaceous laterally, with a patch of setae dorsolaterally; T2 punctate medially; other tergites coriaceous (except for polished band along anterior margin of T2–4), setose (except T2 medially); indications of faint transverse punctures on T4–5.

Variation (♂).—Length 3.0 to 3.7 mm.

Type Material.—Holotype ♀ (CAS No. 15245) and Allotype ♂ (CAS No. 15245a), U.S.A.: CALIFORNIA, Tulare Co., Ash Mtn., Kaweah powerhouse #3, VII-3-1982, from a hydroelectric flume, R. D. Haines, D. J. Burdick, J. A. Halstead. Paratypes: CALIFORNIA, 18 ♀ paratypes with same data as holotype except collected: VII-3-1982, VIII-8, 15-1982, X-1-1982, VII-3, 10, 24-1983, X-8-1983, VI-10-1984, VI-8-1985, VI-1986, one specimen W. F. Peregrin collector (USNM, CNC, AMNH, JAH, RDH). 1 ♀, Tulare Co., Three Rivers, VII-18-1986, Apple maggot trap, R. D. Haines (RDH). 1 ♀, Riverside Co., San Timoteo Cyn., Malaise trap, 10a-3p, IX-9-1974, M. Wasbauer, R. McMaster (CDFA); 1 ♀, Riverside, VII-27-1921, *Euphorbia albomarginata,* Timberlake (UCR); 2 ♀, Riverside, VI-13-1978, J. C. Hall (UCR); 2 ♀, Menifee Valley (hills on west end), 33°39′N, 117°13′W, 1800′ elevation, IX-16–21-1981, pan traps under *Eriogonum* (UCR). 1 ♀, Stanislasus Co., Del Puerto Cyn., Frank Raines Park, 335 m, V-16-1970, P. H. Arnaud, Jr. (CAS). 1 ♀, San Diego Co., San Diego, III-29-1891, F. E. Blaisdell (CAS).

GEORGIA, 1 ♀, Clarke Co., Horseshoe Bend, Athens, Univ. of Georgia Ecol. Inst., VI-26-1967 (UOG).

Nontype material.—CALIFORNIA, 2 ♂, Riverside Co., Riverside, VII-10, 13-1978, J. C. Hall (UCR); 1 ♂, Pinyon Flat Public Camp, 1463 m, VI-30-1968, P. H. Arnaud, Jr. (CAS). 1 ♂, San Bernardino Co., 11 mi N. Goffs, Lanfair Rd., V-25-1977, J. D. Pinto (UCR); 1 ♂, 3 mi W. Lucerne Vly., V-5-1975, J. D. Pinto (UCR). 30 ♂, Tulare Co., Ash Mtn, Kaweah powerhouse #3 (CAS, RDH, JAH). 1 ♀, 2 ♂, Kern Co., China Lake Weapons Center, Lark Seep Lagoon, VI-6–8-1986, D. J. Burdick (CSUF). ARIZONA, 1 ♂, Santa Cruz Co., Patagonia, VII-4-1961, L. R. Breimeier (LCM). MEXICO, SONORA, 3 ♂, San Larios, IX-3-1970, on *Euphorbia,* R. M. Bohart (USU).

Host.—Unknown.

Comments.—The female of this species is most similar to *H. micra* but, *burksi* is longer in length and the ovipositor has the dorsal margin rounded.

Etymology.—The specific name, a noun in the genitive case from a modern personal name, is in honor of Barnard D. Burks (former Chalcidologist with the USDA c/o USNM) who is one of the pioneering researchers in this field and who graciously donated to the Society to fund this publication.

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NOTES ON THE BIOLOGY AND IMMATURE STAGES OF *STENOPA AFFINIS* QUISENBERRY (DIPTERA: TEPHRITIDAE)

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Abstract.—*Stenopa affinis* Quisenberry is reported for the first time from Nevada and from its heretofore unknown, perhaps sole, host plant, *Senecio multilobatus* Torrey and Gray (Asteraceae). This extremely rare, univoltine tephritid overwinters as larvae in mines in crowns of *Se. multilobatus* rosettes without forming galls, unlike its only known congener, *St. vulnerata* (Loew), which forms apical stem galls on basal shoots of a different species of *Senecio*. Pupariation occurs in early summer (June) in vertically oriented, open, frass-lined cells in crowns below ground level. Second and third instar larvae and puparia are described and illustrated for the first time. Distinctive characteristics of the larvae include newly discovered lateral sensory lobes on the gnathocephalon and antero-lateral groupings of five or six morphologically distinct sensilla on each body segment. *Tetrastichus* sp. (Hymenoptera: Eulophidae) were reared from puparia as gregarious endoparasitoids.

Key Words: Nevada, *Senecio multilobatus*, mines, crowns

Stenopa affinis Quisenberry is the much less common, less widespread, and less known of the two species in this genus in North America (Foote and Blanc 1963, Foote 1965, Novak and Foote 1975). The biology and immature stages of *St. vulnerata* (Loew) were described by Novak and Foote (1975), but very little has been published on *St. affinis*. We describe our admittedly incomplete knowledge of this rare tephritid gleaned from field observations and laboratory study of samples collected by RDG at a remote location in western Nevada visited only three times. Continued study of this species under these circumstances was deemed impractical considering the vast amount still to be learned about the biologies and ecology of other, much more common native Tephritidae currently under study by us in California.

Stenopa affinis was described from one male specimen collected in Colorado by Quisenberry (1949). Foote (1965) catalogued a few additional specimens from Arizona and Colorado; whereas, Foote and Blanc (1963) reported no *St. affinis* and only three specimens of *St. vulnerata* from California and noted that the latter species was "found in southern Canada and nearly every state in the United States." The following records represent the first reports of *St. affinis* from Nevada (at a location just across the California border) and from an identified host plant: One female was reared from the crown of a mature *Senecio multilobatus* Torrey and Gray growing in shade under *Populus* spp. on the south-facing bank of a stream in Middle Canyon at 2690-m elevation east of Boundary Peak in the White Mountains, Inyo National Forest, Esmeralda Co., Nevada, on 10 vi 1987. One male and one female also were reared on 27 vii and 14 vii 1989, respectively, from puparia dissected from separate crowns collected at

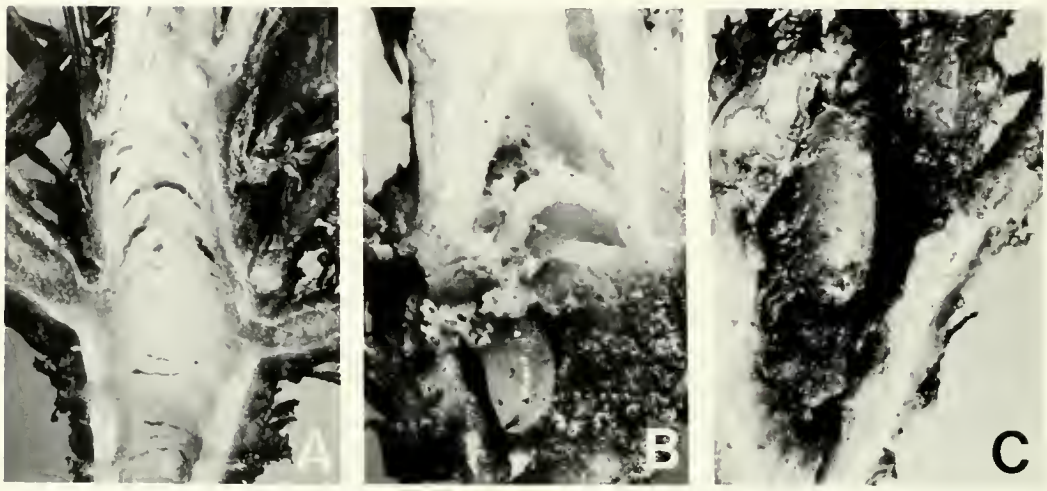

Fig. 1. (A) Longitudinal cross-section through uninfested crown of *Se. multilobatus* (3.9×); (B) second instar larva of *St. affinis* in pith of upper crown of *Se. multilobatus* (7.8×); (C) puparium of *St. affinis* in cell in pith of crown of *Se. multilobatus* (3.1×).

the same location on 25 vii 1989. These three specimens reside in the research collection of RDG.

Stenopa vulnerata was reported from *Senecio aureus* L. by Novak et al. (1967) and Novak and Foote (1975), so the known hosts of both species of *Stenopa* are congeneric. The distribution of *Se. multilobatus* includes Arizona, California, Colorado, and Nevada in the southwestern United States (Munz 1974); *St. affinis* could be monophagous on this host. This contrasts with the widespread distribution of *St. vulnerata* in North America, which Novak and Foote (1975) noted was wider than that of *Se. aureus,* and thus, probably includes other species of *Senecio.* Laboratory dissection in 1988 of 78 rosettes of *Se. multilobatus* sampled at three locations between 3300- and 3400-m elevations on White Mountain on the California side of the border across from the Middle Canyon study site in Nevada detected no *St. affinis*; although, this fly, like its host plant, probably also occurs in the former state.

Another major difference was discovered in the biologies of the two species of *Stenopa.* Novak et al. (1967) and Novak and Foote (1975) reported that *St. vulnerata* larvae form small stem galls near the apices of basal shoots arising from crowns; whereas, *St. affinis* is not a gall former. Instead, the larvae of *St. affinis* mine the parenchyma in the center of the crowns (basal underground stem and upper root) of their biennial or short-lived perennial host plants (Fig. 1A, 1B), without causing detectable tissue proliferation (Fig. 1A, 1B).

The life cycle of *St. affinis* largely was determined from laboratory dissections of 16 (8%) infested crowns of 200 overwintered rosettes sampled from Middle Canyon and nearby Trail Canyon on 19 v and 20 v 1988 and of 10 (20%) infested crowns of 50 postblossom plants sampled in Middle Canyon on 25 vii 1989. Like *St. vulnerata* (Novak and Foote 1975), *St. affinis* is univoltine.

Judging from our plant samples and the adult emergence recorded above, *St. affinis* probably oviposited from mid- to late summer (early August through mid-September) in Middle Canyon. Tracing mines of younger overwintering larvae (Fig. 1B) in 1988 indicated that oviposition occurred in an axil between two basal leaves on a solitary

rosette or on one or more rosettes arising from 2- or 3-year-old crowns. Oviposition also occurred after flowering and fruiting by *Se. multilobatus* had ceased by late July, 1989.

Upon hatching, the larvae tunneled basipetally down the leaf trace into the pith parenchyma, then sinuously downward through the vertical series of whitish septa alternating with narrow, open spaces that form a natural cavity in the upper crown (Fig. 1A). The tunnels continue vertically into the more solid parenchyma of the root pith and are open, smooth-walled, and lined with reddish-brown, fine-grained frass (Fig. 1C). The larvae overwinter as second and third instars, this range probably being reflective of a protracted oviposition period or differential rates of larval growth. Upon resumption of feeding and growth during spring, the larva eventually excavates an open, ellipsoidal, vertically oriented, centrally located, frass-lined cell, 16 of which averaged 10 (range, 7–13) mm long by 4 (range, 3–6) mm wide, where it eventually pupariates (Fig. 1C). An exit tunnel 2–3 mm wide averaging 6 (range, 4 to 13; n = 15) mm in length tapers upward from each cell and ends in a cuticular window formed as a slit between two adjacent stem bases or as a frass plug in the stump of a single central flower stalk. The plug is pushed outward or the window is broken by the emerging adult. The larvae pupariate head-upward, with their posterior ends 3 to 5 mm above the base of the vertical cell; this lower part of the cell often is packed solid with frass. Twenty-two larval tunnels reached a mean depth of 15 ± 0.5 mm ($\bar{x}$ ± SE) below ground level.

Larvae of unidentified genera and species of Curculionidae and Gelechiidae as well as *Melanagromyza* sp. (Diptera: Agromyzidae) also mined the crowns of *Se. multilobatus* at our California and Nevada sample sites. Also, one puparium each collected in 1988 and 1989 yielded gregarious, endoparasitoids identified as *Tetrastichus* sp. (Hymenoptera: Eulophidae).

The adult female pictured in Fig. 2 lived for 49 days caged at room temperature in a clear plastic, 1.1 l, screen-topped container provisioned with two fresh, open capitula of *Aster spinosus* Bentham as sources of pollen and as resting places. Honey was striped on the inner lid, and water was provided via a wick immersed in a basal reservoir. This female and the male reared in 1989 were very active fliers, immediately seeking to fly upwards when freed, and too active to photograph except when confined to a petri dish (Fig. 2). Too few adults were reared to study their courtship and mating behavior, as Novak & Foote (1975) described for *St. vulnerata.*

One second and two third instar larvae and 14 empty or intact puparia dissected from crown samples were used to describe these immature stages using scanning electron microscopy (SEM). Larvae were killed in 70% EtOH serially rehydrated to distilled water, fixed in a 2% solution of osmium tetroxide for 24 h, dehydrated to 100% EtOH, critically point dried, and mounted on stubs with colloidal graphite (Headrick and Goeden, in press). Specimens were examined and micrographs prepared at 15 kV accelerating voltage, unless otherwise noted, using Polaroid 55 P/N film on a JOEL JSM-C35 SEM located in the Department of Nematology, University of California, Riverside, or on a Phillips 515 SEM, located in the Department of Biology. No eggs or first instars were observed. The mature third instar is described in detail using the nomenclature and format adopted by Headrick and Goeden (in press); the second instar description is limited to observed differences.

Third instar.—This relatively large nonfrugivorous tephritid (a single, mature larva measured 5.1 mm long and 1.75 mm wide), is elongate and uniformly cylindrical (Fig. 3A), rather than barrel-shaped as Novak and Foote (1975) described *St. vulnerata.* The

Fig. 2. Adult female of *St. affinis* (8.5×).

integument is transluscent-white with a somewhat greyish cast. The body is smooth dorsally, with two or three folds per segment ventrally.

The mouth-hooks are heavily sclerotized, bidentate, and smooth. The dorsal rib of the median oral lobe tapers to a point anteriorly, and the ventral lobe is laterally flattened, smooth and without ventral papillae (Fig. 3B, arrow). Three cephalopharyngeal skeletons were 0.5 to 0.52 mm long. The gnathocephalon is cone-shaped, rugose, and superficially divided on its anterior face by a medial depression; the anterior edge holds numerous integumental petals dorsally surrounding the mouth-hooks (Fig. 3C, 1). The paired dorsal sensory organs are composed of a single papilla (Fig. 3C, 2); the paired anterior sensory lobes lie dorsal of the mouth lumen and hold the lateral sensory organ, the pit sensory organ and the terminal sensory organ, as is typical among non-frugivorous larval Tephritidae (Headrick, unpublished data).

Another pair of sensory organs are located ventro-laterally on the edge of the gnathocephalon surrounding the mouth lumen (Fig. 3C, 3). These sensory organs are similar in form to the anterior sensory lobes with a ring-like structure bearing a pore sensillum, a papillate sensillum, and a fluted cone-like peg (Fig. 3D, 1, 2, 3). This pair of sensory organs is most likely homologous to the stomal sense organs described for larvae of *Anastrepha ludens* (Loew) (Diptera: Tephritidae) by Carroll and Wharton (1989), and the ventral sense organ of *Musca domestica* (Diptera: Muscidae) larvae described by Chu and Axtell (1972). However, there is enough difference in placement and structural detail to warrant not equating the pair of sensory organs on *St. affinis* with these other described sensory organs until further evidence demonstrates their homology.

The prothorax is rounded, smooth and has several sensilla. The anterior thoracic spiracle is located dorso-laterally on the posterior margin of the prothorax (Fig. 3E, arrow). It projects in a dorso-ventral fan-

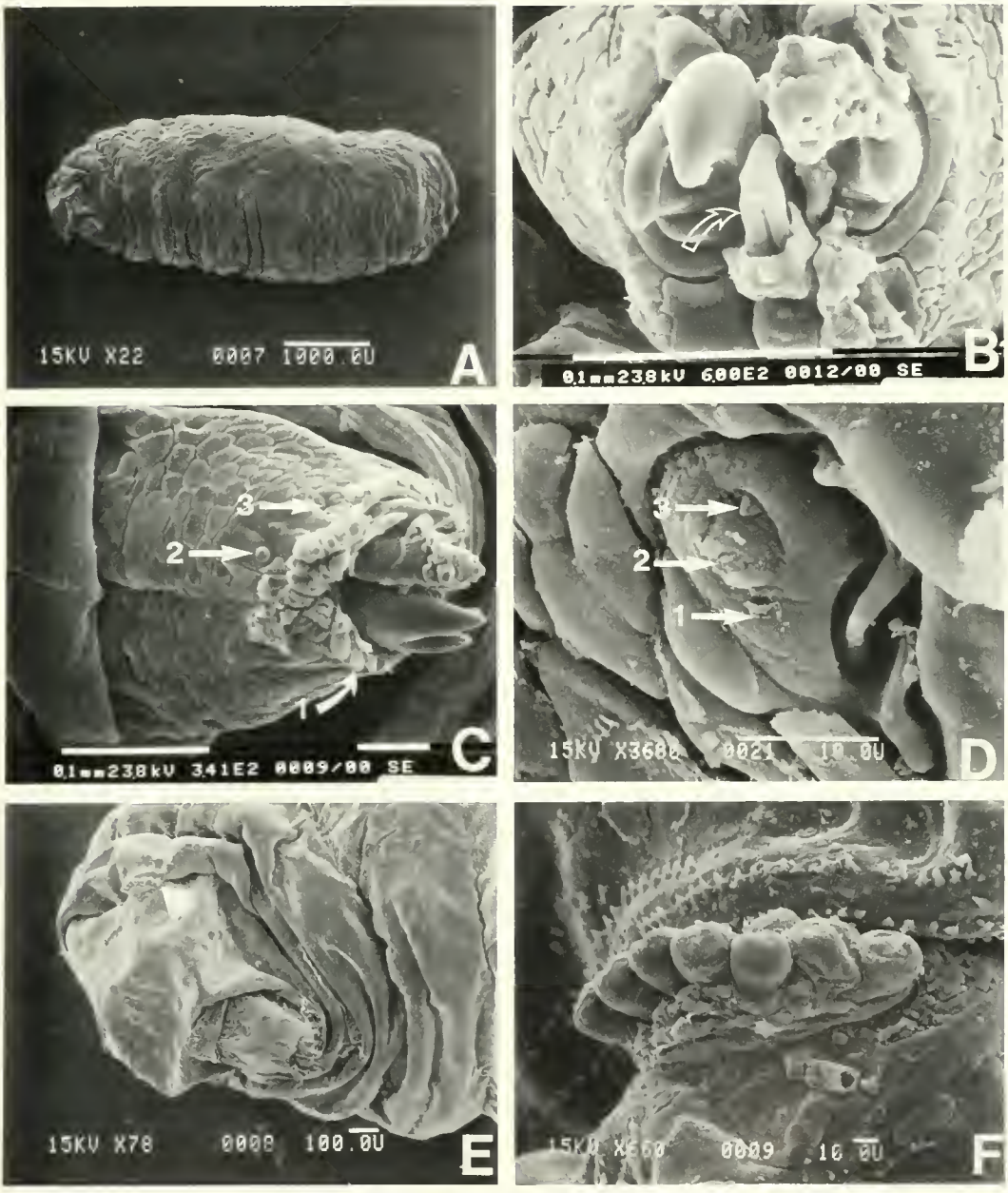

Fig. 3. Third instar larva of *St. affinis*. (A) Habitus; (B) anterior view, mouth region, arrow denotes median oral lobe; (C) gnathocephalon; 1—integumental petals; 2—dorsal sensory organ; 3—lateral sensory organ; (D) lateral sensory organ; 1—pore sensillum; 2—papillate sensory structure; 3—fluted, peg-like structure; (E) anterior end, arrow denotes anterior thoracic spiracle; (F) anterior thoracic spiracle.

shape bearing eight rounded papillae (Fig. 3F). This is distinct from the anterior thoracic spiracle of *St. vulnerata* which bears 24 to 26 scattered finger-like papillae (Novak and Foote 1975).

The body segments are demarcated by rows of minute depressions which circumscribe the body (Fig. 4A, arrow), and the intersegmental bands of acanthae are minute (Fig. 4A). Each segment bears an anterio-lateral grouping of five or six morphologically distinct sensilla (Fig. 4B). The most anterior sensillum is single, wrinkled, and inverted; posterior to this is a group of three wart-like, rounded sensilla with a central pore (Fig. 4C) arranged in a vertical row; posterior to this row are one or two rounded papillate sensilla. These specific types and arrangements of sensilla have not been described for any tephritid larva. Ventrally, each segment also is invested with a pair of rounded sensilla, one on each side of the ventral midline. The caudal end is broadly truncate and bears the posterior spiracular plates dorsal to the transverse midline. Each spiracular plate bears three elongate-oval spiracular rimae and four interspiracular processes.

Second instar larva.—The single second instar examined measured ca. 3 mm in length and ca. 1.5 mm wide (Figs. 1B, 5A). It was translucent white and more barrel-shaped than the third instar. Most structures were similar in size and number to that of the third instar, except for subtle degrees of morphogenesis, which can be quite pronounced between stadia in other tephritid larvae (Carroll and Wharton 1989, Headrick and Goeden in press and unpub. data). The gnathocephalon and mouthparts are similar to that described for the third instar (Fig. 5B, 1). The gnathocephalon is rugose and bears three sensory organs including the lateral sensory organs (Fig. 5B, 2). The anterior thoracic spiracle bears eight somewhat underdeveloped papillae (Fig. 5C).

Puparium.—Fourteen puparia averaged

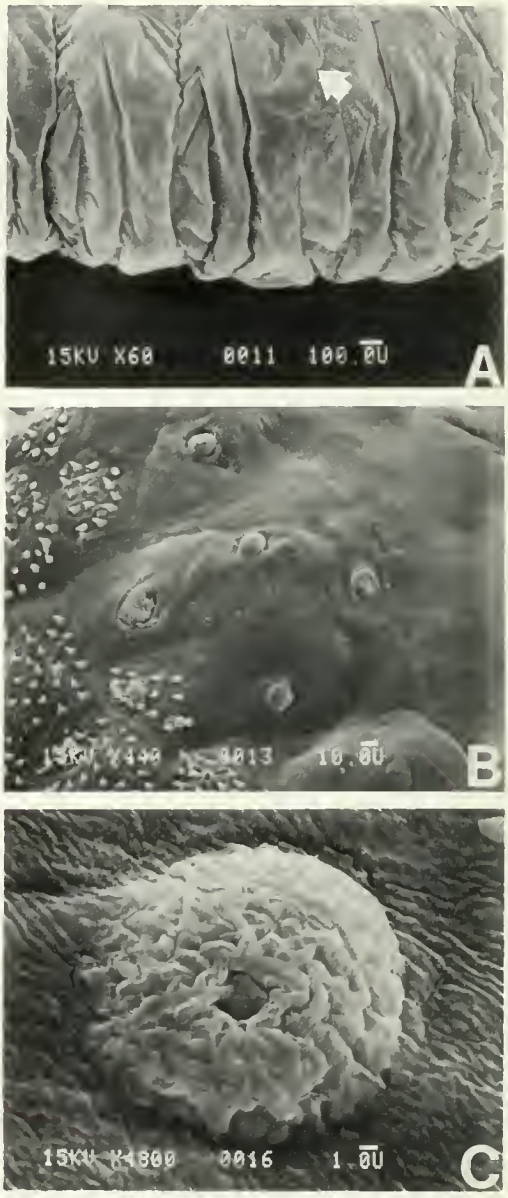

Fig. 4. Third instar larva of *St. affinis*. (A) Venter, arrow denotes depressions along segmental lines; (B) lateral grouping of sensilla; (C) detail of middle, wart-like sensillum.

5.7 ± 0.15 mm in length and 2.5 ± 0.06 mm in widest width. The puparium is translucent, oblong, barrel-shaped, rounded at both ends, and smooth. Prior to eclosion the pharate adult is easily visible through

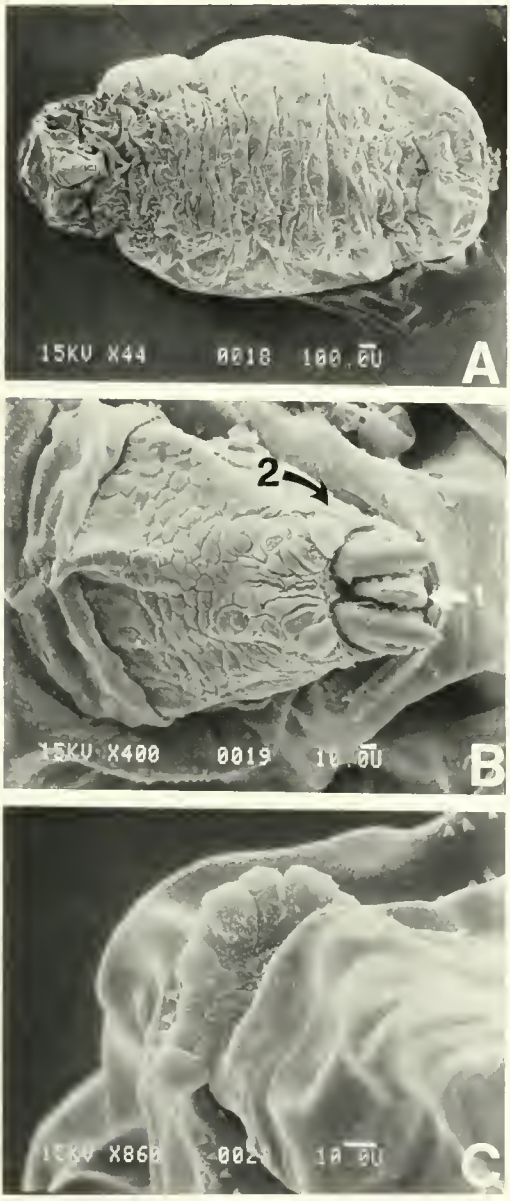

Fig. 5. Second instar larva of *St. affinis*. (A) Habitus; (B) gnathocephalon; 1—median oral lobe; 2—lateral sensory organ; (C) anterior thoracic spiracle.

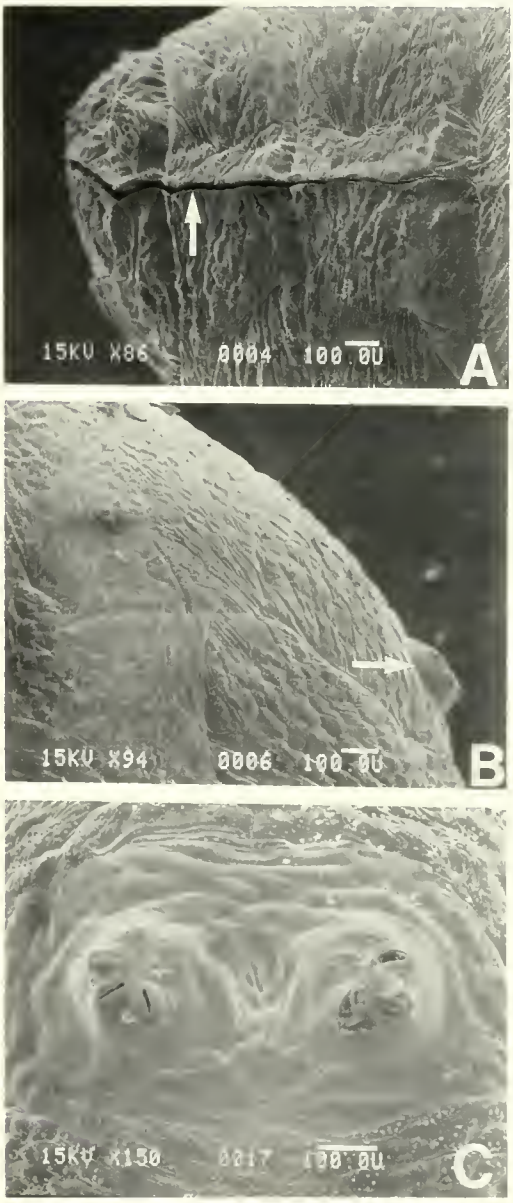

Fig. 6. Puparium of *St. affinis*. (A) Anterior end, arrow denotes lateral fracture line; (B) posterior end, arrow denotes raised posterior spiracles; (C) posterior spiracles.

the puparial integument; it was also noted that the wings of the adults were fully pigmented within the puparia. The anterior end bears the open anterior thoracic spiracles, and the lateral fracture line which extends posteriorly for three segments (Fig. 6A, arrow). The posterior spiracular plates slightly protrude dorsal to the transverse midline (Fig. 6B, arrow); the rimae are elongate-oval; the spiracular slits are ca. 0.05 mm long; and the interspiracular processes are small and lack well-defined blades (Fig. 6C).

Acknowledgments

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THE *ASPHONDYLIA* (CECIDOMYIIDAE: DIPTERA) OF CREOSOTE BUSH (*LARREA TRIDENTATA*) IN NORTH AMERICA

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Abstract.—Fifteen species of gall midges of the genus *Asphondylia* that form complex galls on leaves, stems, or buds of creosote bush are described. Fourteen of the species are new to science, the other is redescribed. One other species that was caught in flight and is similar to the leaf gall makers of *Larrea* is also redescribed. The *Asphondylia* spp. on creosote bush appear to be a monophyletic group and are treated as the *Asphondylia auripila* species group.

Key Words: Complex galls, Southwestern desert, gall midges

Fifteen distinct kinds of complex galls growing on leaves, stems, and buds of *Larrea tridentata* (Sessé & Mocino ex DC.) Cov. (Zygophyllaceae) were found by G. L. Waring during the course of an ecological study of this plant. Each type of gall is formed by a different species of the genus *Asphondylia,* all of them except one new to science. In this paper we describe or redescribe these gall midges and place them in context with one another and with the rest of the genus. The natural history, ecology, and natural enemies of these flies have been or will be treated separately in Waring (1987), Waring and Price (1989a, b), and Waring (in preparation).

Larrea tridentata, or creosote bush, is a dominant member of southwestern desert plant communities from Texas to California (Mabry et al. 1977, Waring 1986). It is a perennial, evergreen shrub, and one of the most drought-tolerant plants in southwestern United States. *Larrea* is restricted to the New World and is one of many taxa of plants and animals that show a disjunct distribution between the southwestern North American and South American deserts. *Larrea tridentata* is the only species of *Larrea* in North America, while four others occur in southern South America (Waring 1986).

Asphondylia is a large, cosmopolitan genus of 247 described species (Foote 1965, Gagné 1968, Gagné 1973, Gagné in press, Gagné in prep., Harris 1980, Skuhravá 1986). To date, 67 species have been described from the Nearctic Region (Gagné in prep.). Almost as many more Nearctic species are known but not yet described (Gagné 1989). Gagné (1989) listed the described and undescribed Nearctic species and their hosts and discussed *Asphondylia* in general. A thorough generic analysis of the tribe (as a supertribe) to which the genus belongs was done by Möhn (1961). The Nearctic species of *Asphondylia* have not been revised since Felt (1916), but recent studies were made of a monophyletic group of eight species that occurs on Chenopodiaceae in California (Hawkins et al. 1986)

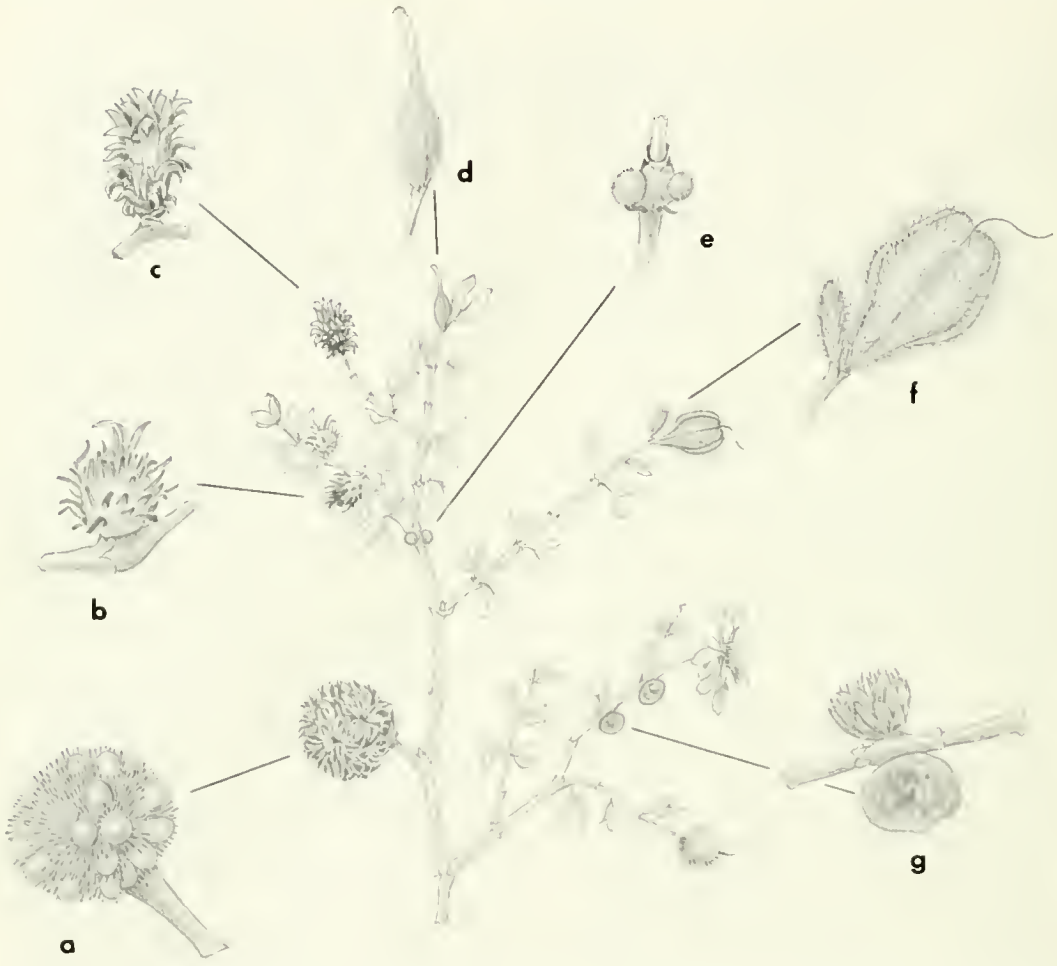


Fig. 1. Stem and bud galls of *Larrea tridentata* formed by *Asphondylia* spp. Sprig of plant in 1×, details of galls in 3×. 1a: Stem gall of *A. auripila*, the detail with outer leaves removed to show the individual cells beneath; b, stem galls of *A. foliosa*; c, stem gall of *A. rosetta*; d, apical bud gall of *A. apicata*; e, node galls of *A. bullata*; f, flower gall of *A. florea*; g, stem galls of *A. resinosa*, the resin of one of the enlarged pair removed to show detail.

and of *Asphondylia websteri* Felt, an apparent generalist known from some Fabaceae and other plants (Gagné and Wuensche 1986, Gagné and Woods 1988). In addition, one of us (RJG) made a survey for this study of certain characters on all known described Nearctic species.

Asphondylia adults are between 1–5 mm in length and are relatively robust with cylindrical antennae, large eyes, and an almost complete covering of scales. They are generally brown to dark brown, but some species, such as *Asphondylia monacha* Osten Sacken and relatives, have black- and white-banded legs and are otherwise covered with black scales. Females have a rigid, protrusible, needlelike ovipositor (Figs. 7, 8) with which they insert their eggs into living plant tissue. Larvae are generally white to yellow, have three instars, and always occur singly, either taking up the entire gall or an individual cell in aggregate galls. The last instar is robust and has a spatula (Figs. 35–47), a hard, brown to black dermal struc-

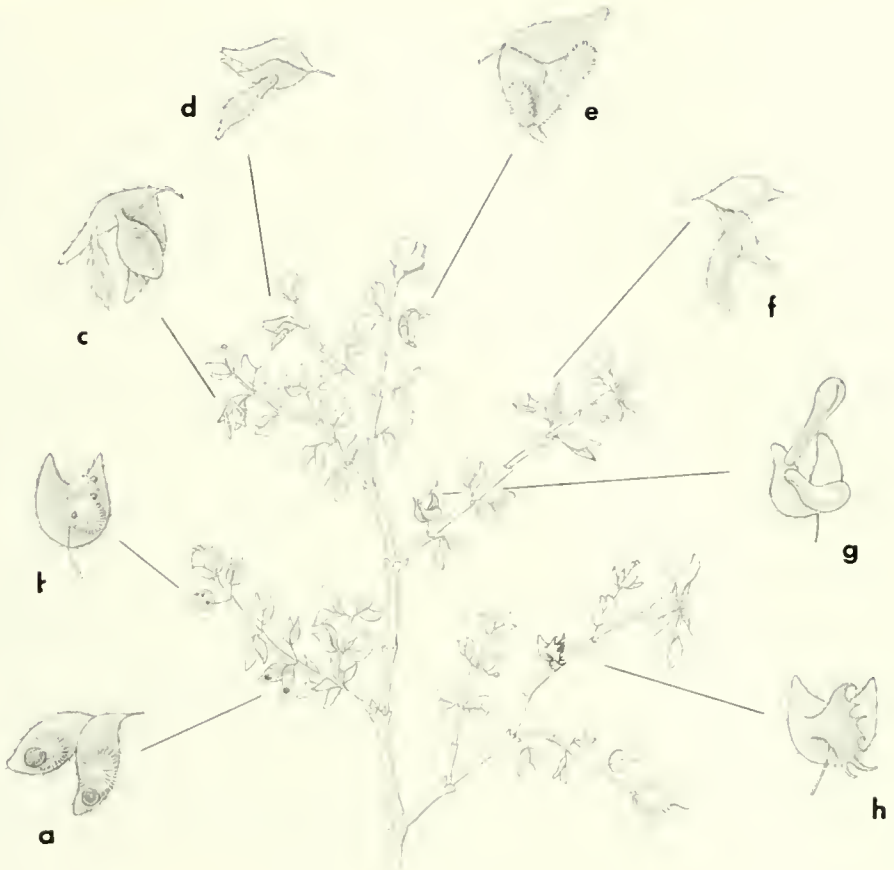


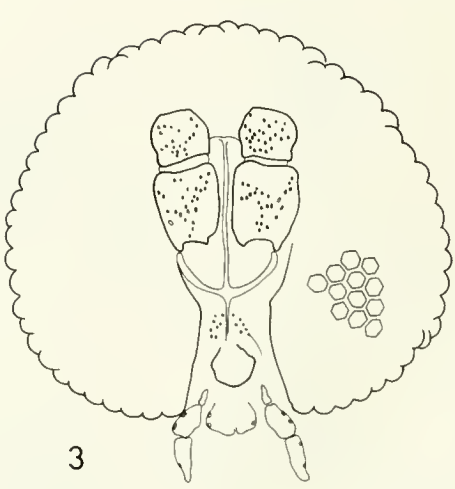
Fig. 2. Leaf galls of *Larrea tridentata* formed by *Asphondylia* spp. Sprig of plant in 1×, details of galls in 3×. 2a: Galls of *A. barbata*; b, galls of *A. villosa*; c, galls of *A. discalis*; d, gall of *A. silicula*; e, galls of *A. pilosa*; f, gall of *A. fabalis*; g, galls of *A. clavata*; h, galls of *A. digitata*.

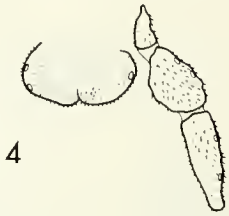
ture on the first segment of the thorax. All species in the genus pupate in the galls. The pupa is also robust, and its integument is hard and brown or black. Its head has horns of various kinds and dorsally the abdomen is covered with spines, all of which serve to effect escape from the galls.

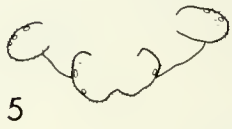
Of the 15 species of *Asphondylia* associated here with as many different kinds of galls on *Larrea*, *Asphondylia auripila* Felt is the only one previously described. One other species, *Asphondylia brevicauda* Felt, is known from a single female without host association. That female is similar to those from six kinds of galls on creosote bush but without associated immature stages cannot be relegated to any one of the six species. It is redescribed here as a sixteenth species but not treated further in our discussion of the *auripila* group.

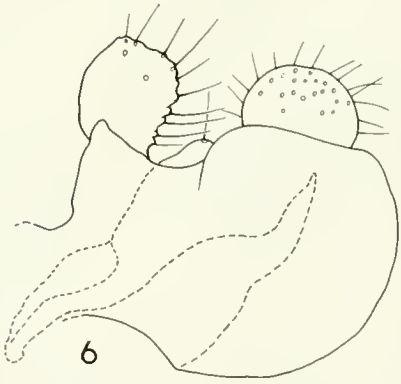
Materials and Methods

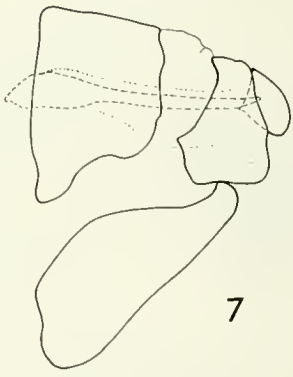
Galls were collected when fully developed and were separated by type. Some galls were cut open to obtain samples of larvae, which were preserved in 70% alcohol. The remainder of the galls were isolated in plastic bags with absorbent tissue paper in order to rear adult gall midges and parasitoids. The bags were kept at room temperature and out of direct light. After adults had emerged, they and their pupal exuviae were kept in

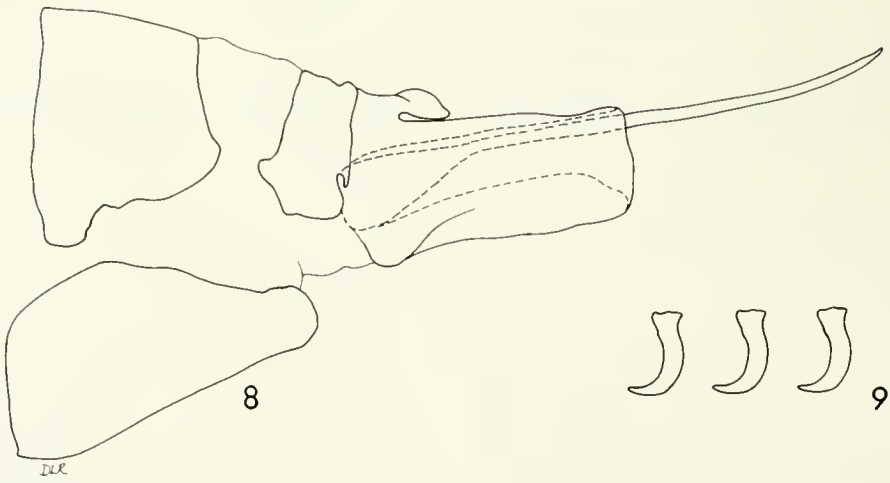




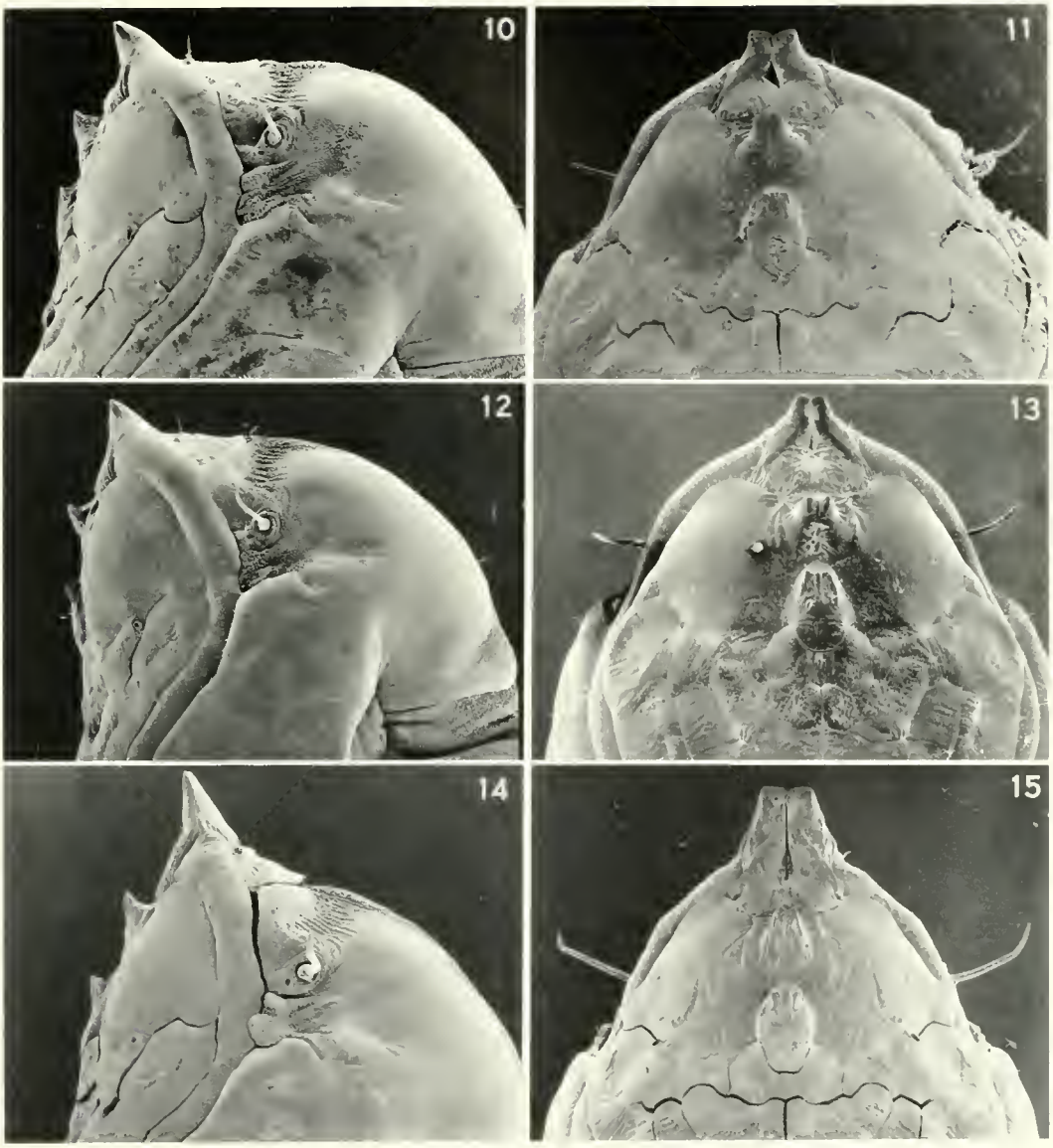








Figs. 3–9. Adult structures of *Asphondylia* spp. 3, Head of *A. clavata*, frontal view. 4, Detail of mouthparts of Fig. 3. 5, Detail of mouthparts of *A. barbata*. 6, Male genitalia of *A. resinosa*, lateral. 7, Abdominal segments 7 to end of female *A. clavata*, lateral. 8, Same, *A. resinosa*. 9, Fore, mid, and hind tarsal claws, *A. resinosa*.



Figs. 10–15. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 10, 11, *A. auripila*. 12, 13, *A. foliosa*. 14, 15, *A. resinosa*.

70% alcohol. Examples of the galls were kept either in alcohol or dry.

For microscopic examination, examples of larvae and adults were mounted on slides in Canada balsam according to the technique outlined in Gagné (1989). Samples of pupae were critical-point dried and placed on stubs for SEM photos. Terminology of adult body parts follows that of McAlpine et al. (1981); larval terminology follows that in Gagné (1989).

The species from *Larrea* are described here in a fashion comparable to that of the species on *Atriplex* in Hawkins et al. (1986) and of *A. websteri* in Gagné and Wuensche (1986). We believe the *Asphondylia* spp. on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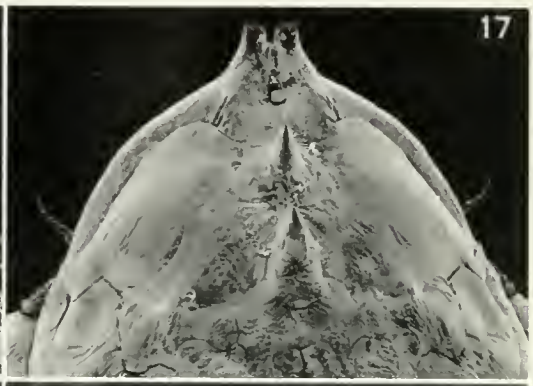
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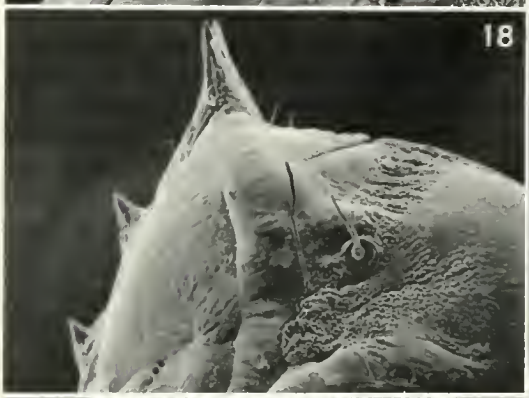
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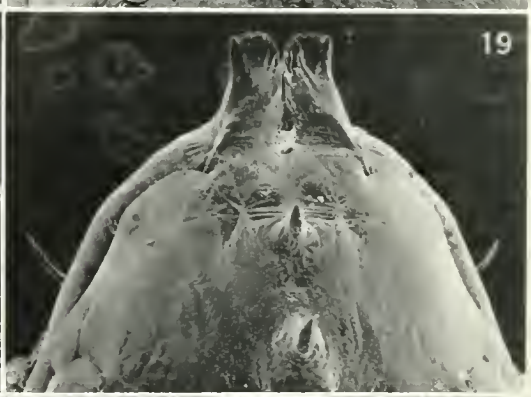
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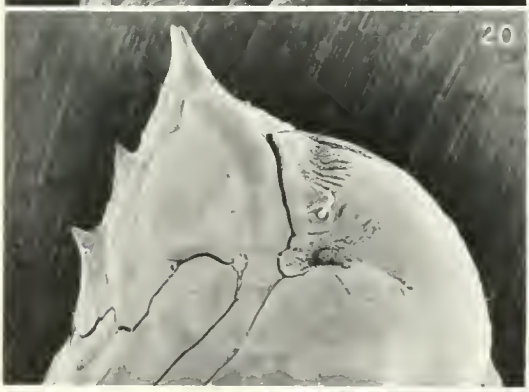
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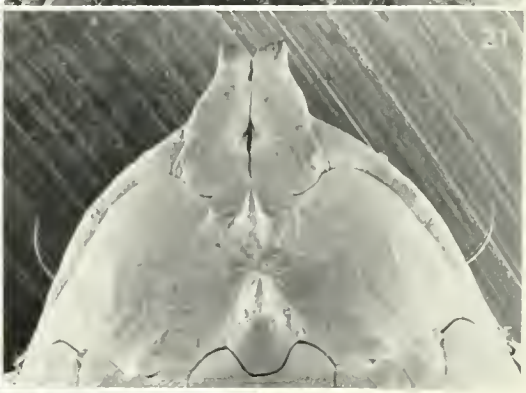
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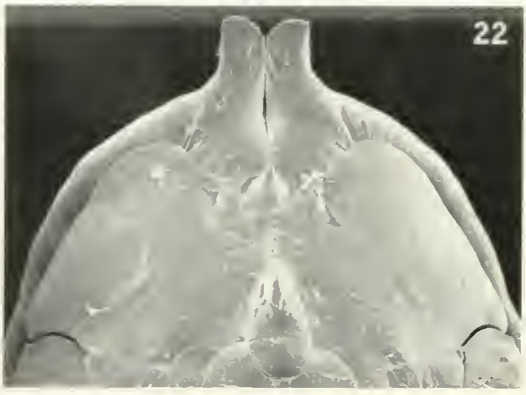
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Larrea to be monophyletic, so will refer to them collectively here as the *Asphondylia auripila* group. Because so many characters are common to all the creosote bush species, a combined description of the group is made at the outset to avoid repetition in the individual descriptions that follow.

The descriptions and redescriptions of these species are in alphabetical order so they can be easily found, but the plates of figures treat the species in natural groupings. All types and other material examined are deposited in the National Museum of Natural History in Washington, D.C.

The 14 new species are given adjectival names that describe some aspect of their galls, either their shape or their position on the plant: apicata = apical; barbata = bearded or hairy; bullata = knobby; clavata = clubshaped; digitata = digitate; discalis = platelike; fabalis = beanshaped; florea = of the flower; foliosa = leafy; rosetta = rosette; pilosa = hairy; resinosa = resinous; silicula = podlike; villosa = hairy.

Description of the *Asphondylia auripila* Species Group

Adult.—*Color:* Eyes black. Face and frons yellowish. Occiput brown beneath covering of long hairs. Antenna brown. Thorax: scutum dark jade green, pruinose; scutellum brown with long setae; pleura brown; wing membrane irridescent, the veins brown; halter yellow to dusky; legs covered with white scales. Abdomen dark brown beneath the thick covering of setae and setiform scales. The setae and setiform scales covering the thorax and abdomen may be silvery (*clavata, pilosa, barbata,* and *rosetta*) or golden (*auripila* and *resinosa*) (not determinable in most species because most available adults were preserved in alcohol instead of dry on pins).

Head (Figs. 3–5): Antenna: scape broadest distally, 1.6–1.8 times length pedicel, pedicel about as wide as long; first flagellomere 2.1–2.3 times length of scape, evenly cylindrical. Eye facets close together, hexagonoid. Frons with 5–20 setae per side, variable in number within a species. Labellum reduced in size, laterally with 0–4 (usually 2–3) setae and setulose, and medially with 4–6 short, basiconic setae. Palpus 1 or 2–3 segmented: when 1 segmented, usually elongate spherical, tapering at the apex, and with 2–5 scattered setae; when 3 segmented, first segment always short and narrower than the second and with 0–3 setae, and the second and third segments sometimes fused or only partly separated, the second widest and usually shorter than the third, which tapers to a pointed end; second and third segments each with 2–10, mostly lateral setae.

Thorax: Wing length 1.5–4.7 mm. Scutum with 2 dorsocentral and 2 lateral rows of long setae mixed with setiform scales. Anepisternum with scales on dorsal half, anepimeron covered with scales. Claws (Fig. 9) of all legs and both sexes subequal in size and similar in shape, as long as empodia.

Abdomen: Male terminalia as in Fig. 6, homogeneous within the species group. Ovipositor (Figs. 7, 8) 1.0–2.7 times as long as seventh sternite.

Pupa.—Antennal horns variably shaped (Figs. 10–34). Upper frontal horn simple or bifid. Lower frontal horn simple or trifid. Prothoracic spiracle usually short, curved anteriorly, but shaped otherwise on one species. Abdominal tergites 2–8 each with,

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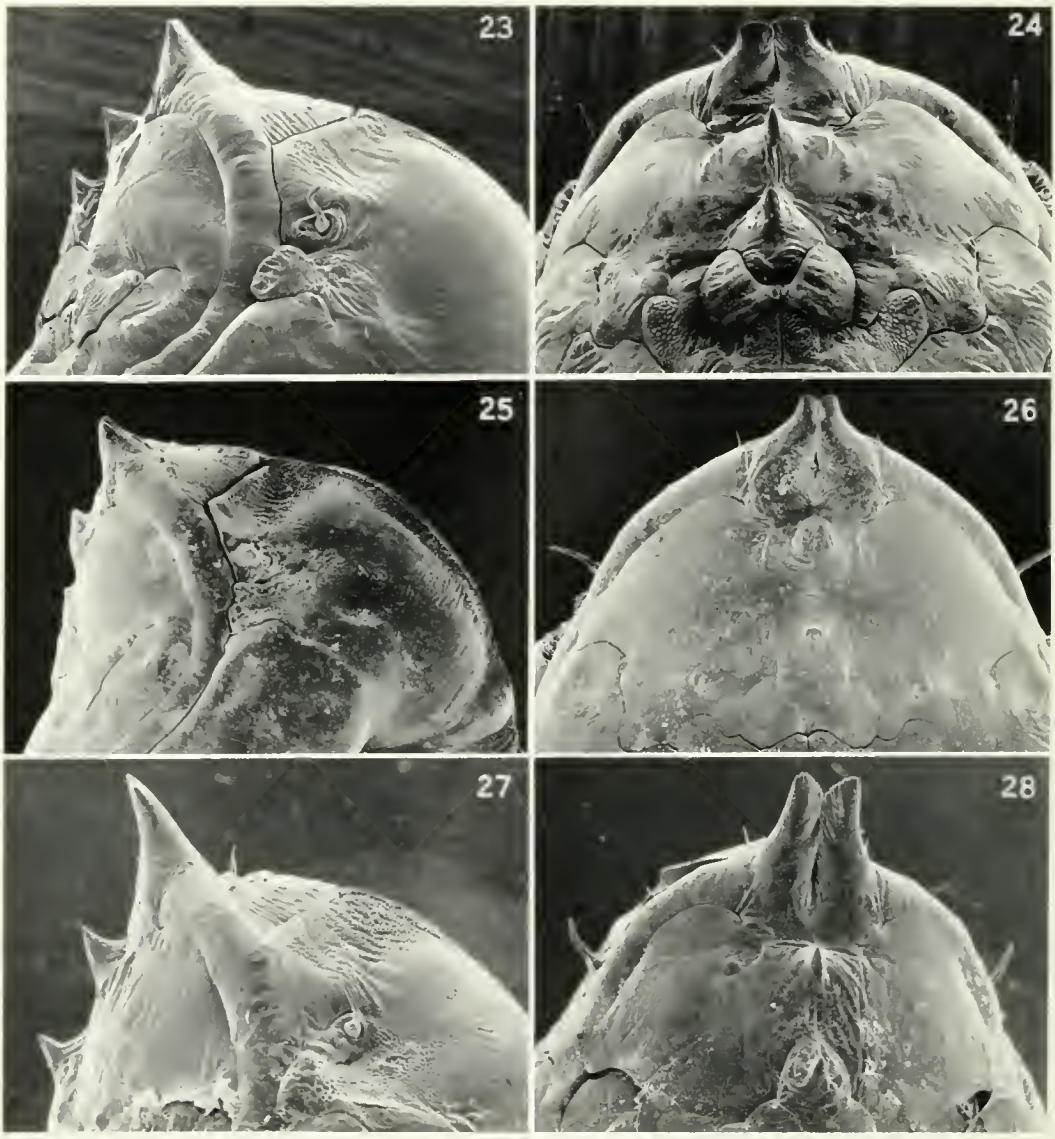
Figs. 16–22. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right and at bottom. 16, 17, *A. rosetta.* 18, 19, *A. apicata.* 20, 21, *A. florea.* 22, *A. villosa.*

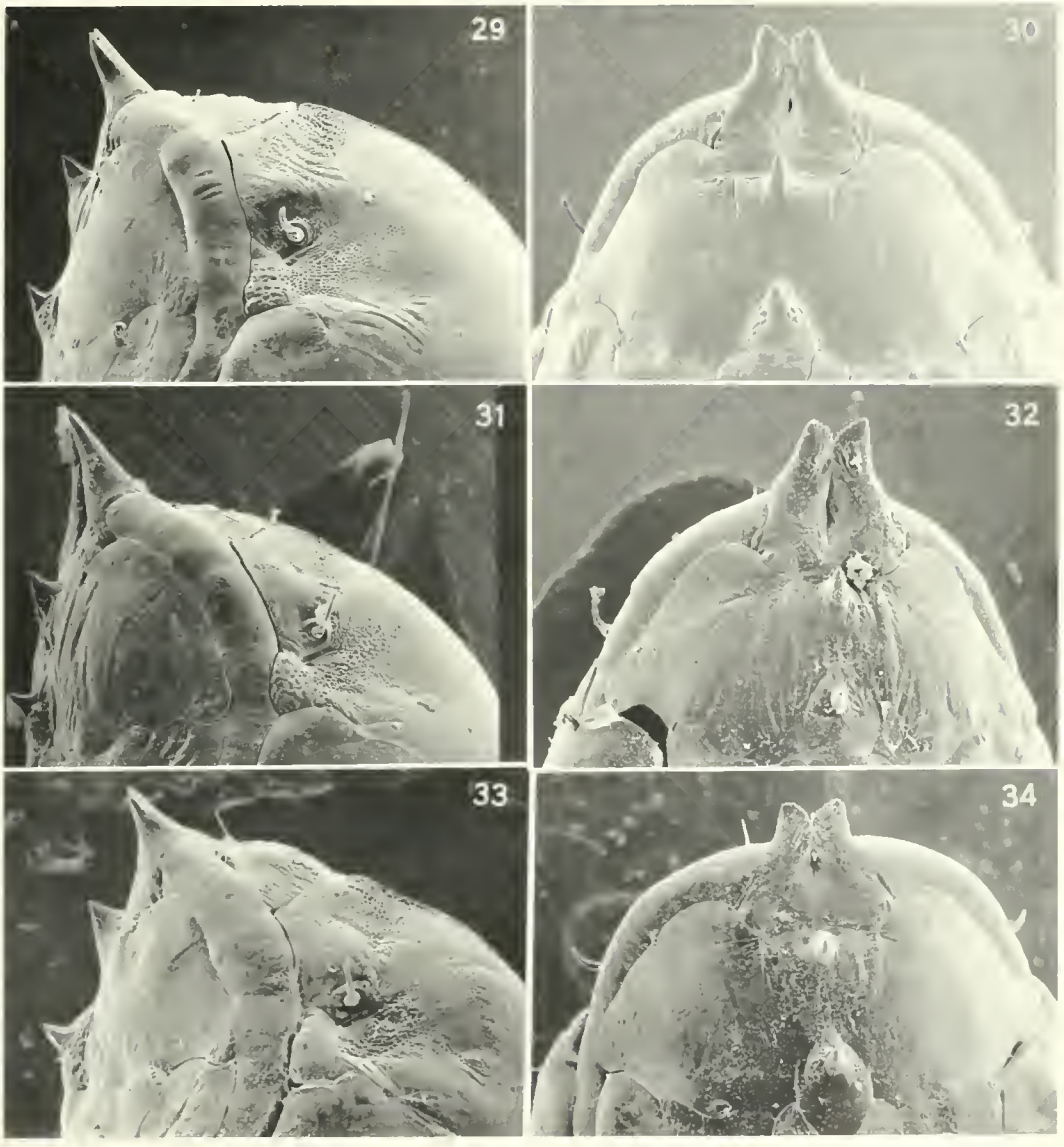


Figs. 23–28. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 23, 24, *A. bullata*. 25, 26, *A. pilosa*. 27, 28, *A. digitata*.

from posterior margin, a row of stout spines, a bare space, another row of stout spines followed by scattered, much smaller spines, these diminishing in size and growing sparser toward anterior margin of sclerite.

Larva.—Papillar pattern as for *Asphondylia* (Möhn 1955, 1961) but with only 2 or 3 ventral thoracic papillae instead of the primitive 6 in 2 groups of 3 each per side and with the terminal papillae reduced to 1 pair, which are greatly reduced and usually difficult to detect. Spatula various (Figs. 35–47), some species having the large spatula with 4, subequal, anterior teeth, but most showing some reduction in area and change in shape. The area around the spatula may or may not be sclerotized and pigmented.

Remarks.—*Asphondylia clavata* and *A.*



Figs. 29–34. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 29, 30, *A. discalis*. 31, 32, *A. fabalis*. 33, 34, *A. silicula*.

pilosa are indistinguishable from one another, as are *A. barbata* and *A. villosa*, but each of the four forms a distinct gall. We treat these four species as distinct, presuming that the different galls are a function of differences in the larval salivary secretions that direct the shape of the galls. Those two pairs of species and the remainder of the species from each of the other kinds of galls are distinct on the basis of some anatomical characters.

We give no key to species of the *auripila* group. There is little use in trying to sort adults caught in flight when they are so similar to other asphondylias and when so many species of the genus are still undescribed. The best way to identify these species is by their distinctive galls as drawn in Figs. 1

and 2. If a larva or pupa is associated with the gall, it would be a good idea to confirm the gall determination by comparing the larval spatula or pupal head with the figures given in this paper for the particular species.

Asphondylia apicata Gagné, New Species

Diagnosis.—This species forms an apical leaf bud gall (Fig. 1d). The spatula (Fig. 40) resembles slightly those of *A. florea* (Fig. 46) and *A. rosetta* (Fig. 39), but the pupal antennal horn of *apicata* (Fig. 19) is wider and more splayed than in the other two species. The ovipositor of all three species is approximately as long, somewhat elongate for the *auripila* group.

Description.—*Adult:* Wing length: male, 2.7 mm (n = 1); female, ? mm (n = 1 with teneral wings). Labellum with 1–3 setae. Palpus 3 segmented, first segment smallest with 0–1 setae, third segment longer than the second and pointed apically, each with 1–3 setae laterally. Ovipositor 2.4 times as long as seventh sternite, curved dorsally at tip.

Pupa (Figs. 18, 19): Antennal horns long, flattened dorsoventrally, broad and serrate anteriorly in frontal view. Upper and lower frontal horns simple, the lower smaller than the upper in lateral view. Prothoracic spiracles short, curved.

Last instar: Spatula (Fig. 40) with 2 rounded, anterior teeth; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (specimen on left under left cover slip on slide), from apical leaf bud gall on *Larrea tridentata,* dog track, Black Canyon City, Arizona, 2-10-88, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 2-10-88 (7 pupae, 4 larvae); Interstate Hwy 17, Carefree exit, 10 mi N Phoenix, 9-15-87 (3 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (5 pupae), 3-1-81 to 5-1-81 (6 pupae, 7 larvae), 9-15-85 (♂, ♀, 3 larvae). CALIFORNIA: Death Valley National Monument, 2-17-69, J. Wheeler (pupa).

Asphondylia auripila Felt

Asphondylia auripila Felt 1907: 14.

Diagnosis.—This species forms a leafy stem gall that is always found in a large aggregation (Fig. 1a). Several characters are common to *auripila, resinosa* and *foliosa,* including the large size, the bifid upper and trifid lower frontal pupal horn, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. The pupa of *auripila* (Figs. 10, 11) resembles more closely that of *foliosa* with the shorter antennal horn and prothoracic spiracle, but the two differ in the width of the pupal horn.

Description.—*Adult:* Wing length: male, 4.7 mm (n = 1); female, 4.5–4.9 mm (n = 4). Labellum with 1–5 setae. Palpus 3 segmented, the first smallest with 0–1 setae, the second and third sometimes partially fused, each with 2–7 setae, mostly laterally. Ovipositor 1.4 times as long as seventh sternite (n = 3), curved dorsally at tip.

Pupa (Figs. 10, 11): Antennal horns short, nearly rectangular in frontal view. Upper frontal horns large but shallowly bifurcate, lower frontal horn wide, weakly trifurcate.

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Figs. 35–40. Spatulas and associated dermal structures of *Asphondylia* spp. larvae. 35, *A. clavata.* 36, *A. resinosa.* 37, *A. foliosa.* 38, *A. auripila.* 39, *A. rosetta.* 40, *A. apicata.*

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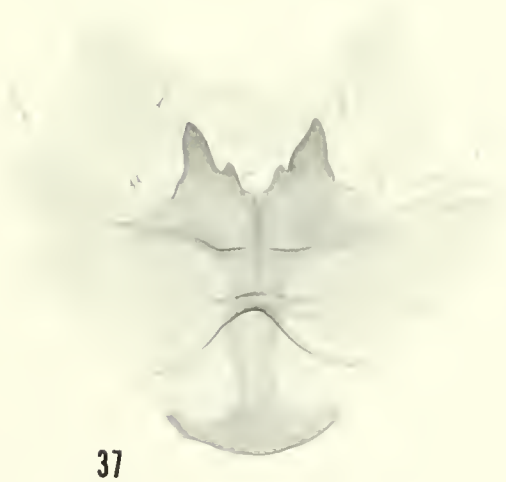

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Prothoracic spiracles short, not recurved apically.

Last instar larva: Spatula (Fig. 38) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the outer; lateral edge of anterior margin of spatula curved laterally; area surrounding spatula only weakly sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Types.—Lectotype male, here designated, emerged from globular, green gall growing at the junction of branchlets of *Larrea tridentata*, collected 1-8-1897, Tucson, Arizona, H. G. Hubbard, emerged 2-6-1897, USDA #7320, USNM Type #29221, on slide. Paralectotype, 1 male, also on slide, same data as lectotype.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (2 ♂, 2 ♀, 18 pupae, 6 larvae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (3 pupae), 8-29-80 (♂, 2 ♀, 5 pupae, larva), 3-1-81 to 5-1-81 (4 pupae, larva), 8-23-83 (11 pupae, 13 larvae), 9-15-86 (2 ♀, 3 pupae, 9 larvae); Tucson (type series; see under type heading). CALIFORNIA: Victorville, 4-4-1918, E. Bethel, Felt notebook #a2891 (♂). MEXICO, SINALOA: Caborca, Lukeville Rd., 1-10-63 (2 larvae). TEXAS: Carlsbad Hwy, 10-6-1940, R. A. Alexander.

Asphondylia barbata Gagné, New Species

Diagnosis.—This species and *villosa* are indistinguishable, but their galls, although showing some resemblance, are distinctly different. Both are squat leaf galls with a rugose, hairless patch at the base. That of *villosa* is covered for almost its entire length with long hair (Fig. 1b), while that of *barbata* is covered for only slightly more than half its length with short hair. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long, wide, apically serrate antennal horn, and simple, large frontal horns. The spatula has two elongate teeth but has a short shaft.

Description.—*Adult:* Wing length: female, 1.5–1.7 mm (n = 4). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.1 times as long as seventh sternite (n = 4).

Pupa (as in Fig. 22): Antennal horns long, flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, of approximately the same length. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (as in Fig. 42) with 2 prominent, long teeth almost as long as the rest of the shaft; area surrounding spatula not modified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from hairy leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-15-87 (pupa); Hwy Alt. 89, 1 mi E Cottonwood, 8-15-87 (2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (5 pupae, 12 larvae), 9-15-82 (♀), 8-1-83 (2 ♀), 8-31-83 (3 larvae).

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Figs. 41–47. Spatulas and associated dermal structures of *Asphondylia* spp. larvae. 41, *A. bullata*. 42, *A. barbata*. 43, *A. fabalis*. 44, *A. silicula*. 45, *A. discalis*. 46, *A. florea*. 47, *A. digitata*.

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A. auripila species group																		
Leaf Galls									Stem Galls			Bud Galls						
clavata	*pilosa*	*barbata*	*digitata*	*discalis*	*fabalis*	*silicula*	*villosa*	*auripila*	*foliosa*	*resinosa*	*apicata*	*bullata*	*florea*	*rosetta*	*atriplicis* group	*websteri*	Other *Asphondylia*	
2	2	1	1	1	1	1	1	3	3	3	2	2	2	2	2,3	2,3	1,2,3	1. Wing length short (1), medium (2), or long (3).*
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	0	2. Labella large with many setae and covered with setulae (0) or reduced in size, with sparse vestiture (1) or without (2).
0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	3. Palpus with three segments (0) or one (1).
1	1	1	1	1	1	1	1	2	2	2	3	3	3	3	2	3	2,3	4. Ovipositor short (1), medium (2), or long (3).*
1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1,2	5. Upper frontal horn simple (1) or bifid (2).*
1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	2	2	1,2	6. Lower frontal horn simple (1) or trifid (2).*
0	0	2	2	2	2	2	2	1	1	1	2	2	2	2	0	0	0	7. Spatula with only inner teeth reduced (1) or with reduced teeth and shaft (2).*
0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	8. Area around spatula pigmented (0) or unpigmented (1).
1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	0	9. Lateral papillae reduced from five pairs (0) to three pairs (1) or two (2).
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	10. Terminal papillae reduced from four to two pairs (0) or one pair (1).

Fig. 48. Character matrix of selected characters for the *Asphondylia auripila* species group and three other units, the *A. atriplicis* species group, *A. websteri*, and other Nearctic *Asphondylia*. Similar species are grouped together to show patterns more readily. Characters 1–4 are of the adult, 5–6 of the pupa, and 7–10 of the larva. For those characters followed by an asterisk no polarity is implied and the numbers in the matrix indicate only character states observed (1, 2, 3). For those characters without an asterisk, 0 indicates a plesiomorphic character state and 1 and 2 apomorphic character states.

Asphondylia brevicauda Felt

brevicauda Felt 1908: 295 (*Asphondylia*).

Diagnosis.—This species, known from one female caught in flight, could fit any one of several species treated as new here, viz. *barbata, digitata, discalis, fabalis, silicula,* and *villosa.* Because larvae and pupae are needed to distinguish among these species, *brevicauda* cannot be referred with certainty to any particular one of those gall makers. It would be expeditious to apply the name *brevicauda* to one of them. Then, we would not have to carry the name *brevicauda* as an available but meaningless entity. Nevertheless, it would not be scientific to apply such a name at random to a taxon to which it did not certainly belong.

Description.—*Adult:* Wing length: female, 1.9 mm (n = 1). Labellum with several setae (obscured on specimen). Palpus with one segment bearing several setae. Ovipositor 1.1 times as long as seventh sternite.

Male, pupa and larva: Unknown.

Holotype.—Female, Fort Yuma, Arizona, 9-4, Coll. [H. G.] Hubbard, USNM Type No. 29219, Felt #c1040, type deposited in U. S. National Museum. No additional data have been found to indicate whether this fly was reared or only caught in flight. The H. G. Hubbard notebooks in the Smithsonian Archives were searched in vain for further information under the dates of Sept. 4 and April 9 of the years Hubbard traveled to Arizona, and there is no code number 9-4 in the Hubbard card files remaining with the Systematic Entomology Laboratory.

Asphondylia bullata Gagné, New Species

Diagnosis.—This species forms a short, socketed stem gall (Fig. 1e). The spatula (Fig. 41) is unique in the *auripila* group because it has four teeth but lacks the surrounding sclerotization present in all the other stem gall makers. The pupa is unique for the short distance between the frontal horns. The ovipositor is the longest in the *auripila* group.

Description.—*Adult* (female only): Wing length: female, 2.1 mm (n = 3). Labellum with 1–3 setae. Palpus 3-segmented, the first smallest with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 3–5 setae laterally. Ovipositor 2.8 times as long as seventh sternite (n = 3), curved dorsally at tip.

Pupa (Figs. 23, 24): Antennal horns short, broad anteriorly. Upper and lower frontal horns simple and about as long as antennal horns; distance between frontal horns uniquely short.

Last instar larva: Spatula (Fig. 41) with 4 anterior teeth, pair of short teeth medially and large one on either side, with long and narrow shaft not surrounded by sclerotized and pigmented area. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (specimen under left coverslip on slide), from stem gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 9-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-30-87 (2 pupae); Diamond Creek, river mile 225, Grand Canyon National Park, 1-5-88 (pupa); Saguaro National Monument, East, 20 mi E Tucson, 3-2-80 (♀, 3 pupae), 1-15-81 (2 ♀, 4 pupae), 3-4-81 (pupa), 9-31-83 (3 larvae).

Asphondylia clavata Gagné, New Species

Diagnosis.—This species and *pilosa* are indistinguishable. Galls of the two species have the same general form except that that of *clavata* is smooth (Fig. 2g), while that of *pilosa* has a thick covering of hair (Fig. 2e). The two species are unique among the *auripila* group for the presence on the larva of four subequal anterior teeth on the spatula

and three pairs of lateral papillae on each thoracic segment (Fig. 35). As with all the leaf galling asphondylias on *Larrea,* their ovipositors are among the shortest of the *auripila* group. The pupal antennal horn is shortened, the upper frontal horn is still wide enough to indicate a reduction from a bifid form, and the lower frontal horn is much reduced.

Description.—*Adult:* Wing length: male, 2.3–3.1 mm (n = 5); female, 2.6–2.9 mm (n = 7). *Color:* setae and long setiform scales silvery. Labellum with 2–3 setae. Palpus with 3 segments, the first smallest with 0–2 setae, the second and third subequal in length with 2–5 setae laterally, the third tapering to pointed apex. Ovipositor 1.0 times as long as seventh sternite (n = 6).

Pupa (as in Figs. 25, 26): Antennal horn short and tapered to rounded apex. Upper frontal horn short, simple, and wide. Lower frontal horn short, barely serrate.

Last instar larva: Spatula (Fig. 35) with 4 anterior teeth, the inner pair slightly shorter than the outer; area surrounding spatula sclerotized and pigmented. Three ventral papillae present on each side of thoracic segments, one singlet and one pair, seta of the singlet longest.

Holotype.—Larva (one of five specimens under cover slip on slide, the specimen at lower right), from clavate gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-84 (2 ♂, 3 ♀, 10 pupae, 16 larvae) and 3-26-88 (8 pupae, 2 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 8-18-86 (♀, 14 pupae, 3 larvae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (5 pupae) and 3-23-88 (5 pupae, 3 larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-10-80 (7 pupae, 2 larvae), 8-29-80 (♀, 5 pupae, 2 larvae), 4-15-82 (3 ♂, 4 ♀), 8-31-83 (♂, 2 ♀, 5 pupae, 18 larvae), and 8-16-84 (2 ♂, 3 ♀, 12 pupae, 3 larvae); Tucson, 4-4-59, M. Adachi (♀, pupa). CALIFORNIA: Los Angeles (no other data; galls only). BAJA CALIFORNIA: 3-4-89 (3 larvae).

Asphondylia digitata Gagné, New Species

Diagnosis.—This species forms a digitate, bilaterally flattened gall on the under surface of the leaf (Fig. 2h). As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple, large frontal horns. The shape of the spatula (Fig. 41) is unique for its splayed anterior margin.

Description.—*Adult* (only females available): Wing length: female, 2.1 mm (n = 1). Labellum with 1–2 setae. Palpus 1 segmented with 1–2 setae. Ovipositor 1.1 times as long as seventh sternite (n = 2).

Pupa (Figs. 27, 28): Antennal horn elongate, serrate anteromedially. Upper and lower frontal horns simple, long, pointed.

Last instar larva: Spatula (Fig. 47) deeply divided anteriorly, the resulting sections splayed, each with a pair of subequal teeth; area surrounding spatula not sclerotized or pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of two specimens under cover slip on slide, the specimen at right), from flat, digitate leaf gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: Parashant Canyon, river mile 198, Grand Canyon National Park, 3-20-1987 (2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-10-80 (♀, 5 pupae), 8-29-80, (♀, 6 pupae), 3-1 to 5-10-81 (pupa), 3-4-81 (6 pupae, 6 larvae), and 8-15-85 (3 pupae, lar-

va). CALIFORNIA: Los Angeles (no other data; galls only).

Asphondylia discalis Gagné, New Species

Diagnosis.—This species forms a circular, bilaterally flattened gall on the under surface of the leaf (Fig. 2c). This species resembles *silicula* except for a longer pupal antennal horn. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple, large frontal horns. The spatula (Fig. 44) is blunt, occasionally slightly bifid anteriorly.

Description.—*Adult* (teneral, removed from pupa): Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor subequal in length to seventh sternite (teneral).

Pupa (Figs. 29, 30): Antennal horns flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, equally long. Prothoracic spiracles curved.

Last instar larva: Spatula (Fig. 45) two blunt, slightly serrate lobes anteriorly divided only slightly, or not at all to resemble *silicula*; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of three specimens under cover slip on slide, the specimen at right), from platelike leaf gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (3 pupae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (3 pupae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (2 pupae), 8-29-80 (2 pupae), 3-1-81 to 5-1-81 (6 pupae, 6 larvae), 3-13-87 (♂, ♀, 5 pupae, 2 larvae).

Asphondylia fabalis Gagné, New Species

Diagnosis.—This species forms a bean-shaped gall on the under surface of the leaf (Fig. 2f). As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple frontal horns. The spatula (Fig. 43) has a short shaft and two large, widely separated anterior teeth.

Description.—*Adult:* Wing length: male, 1.6–1.7 mm (n = 2); female, 1.6–1.8 mm (n = 3). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.0 times as long as seventh sternite (n = 3).

Pupa (Figs. 31, 32): Antennal horn long, broad and serrate anteromedially. Upper and lower frontal horns simple, the lower smaller. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 43) with 2 prominent teeth spread far apart and 2 tiny, inner teeth; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (leftmost of three specimens under left cover slip on slide), from stem gall on *Larrea tridentata,* dog track, Black Canyon City, Arizona, 9-15-87, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (6 pupae, 8 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 4-15-84 (2 pupae, 2 larvae; Parashant Canyon, river mile 198, Grand Canyon National Park, 10-1-86 (2 ♂, 3 ♀, 7 pupae, larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (4 pupae, larva).

Asphondylia florea Gagné, New Species

Diagnosis.—This species forms a cylindrical to pear-shaped flower gall (Fig. 1f).

The spatula (Fig. 46) shows a resemblance to that of *apicata* and *rosetta,* but both the anterior teeth and the entire spatula are longer in *florea.* The pupal antennal horn (Fig. 21) narrows anteriorly, as does that of *rosetta,* but that of *florea* is longer and is wider anteriorly. The ovipositor in all three species is approximately as long, somewhat elongate for the *auripila* group.

Description.—*Adult:* Wing length: male, 2.6–2.8 mm (n = 4); female, 2.5–2.7 mm (n = 4). Labellum with 1–2 setae. Palpus 3 segmented, the first segment with 0 setae, the second and third subequal in length, each with 1–3 setae laterally. Ovipositor 2.1 times as long as seventh sternite (n = 4).

Pupa (Figs. 20, 21): Antennal horns long, flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, equally long. Prothoracic spiracles normal, curved anteriorly.

Last instar larva: Spatula (Fig. 46) with 2 prominent, rounded teeth, and slight projection between; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from flower gall on *Larrea tridentata,* Parashant Canyon, river mile 198, Grand Canyon National Park, Arizona, 5-15-88, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (24 pupae, 3 larvae); Parashant Canyon, river mile 198, Grand Canyon National Park, 5-15-88 (4 ♂, 4 ♀, 6 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-4-81 (2 pupae), 4-10-84 (♂, 2 pupae); Tucson, 4-4-59, M. Adachi (pupa).

Asphondylia foliosa Gagné, New Species

Diagnosis.—This species forms a short, leafy stem gall (Fig. 1b). Such galls are never found in aggregate as are those of *auripila.* This species has several characters in common with *auripila* and *resinosa,* including the large size, the bifid upper frontal pupal horn and trifid lower, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. This species differs from the other two in the apically narrowed antennal horn.

Description.—*Adult:* Wing length: male, 3.2–3.5 mm (n = 4); female, 3.4–3.7 mm (n = 4). Labellum with 1–2 setae. Palpus usually 3-segmented, the first smallest with 0–2 setae, the second and third sometimes not completely separated, each with 5–10 setae, mainly laterally. Ovipositor 1.4 times as long as seventh sternite (n = 2), curved dorsally at tip.

Pupa (Figs. 12, 13): Antennal horns short, rounded in frontal view. Upper frontal horns bifurcate, lower frontal horn shorter but trifurcate, the middle projection shorter than the laterals. Spiracular horn short, curved anteriorly.

Last instar larva: Spatula (Fig. 37) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the 2 outer; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen in middle of upper row), from solitary, foliaceous stem gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-23-1983, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (larva); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 9-15-87 (larva); Parashant Canyon, river mile 198, Grand Canyon National Park, 8-20-1984, (3 larvae); Saguaro National Monument, East, 20 mi E Tucson, 8-11-80 (3 pupae), 8-23-83 (11 pupae, 8

larvae), 8-18-86 (4 ♂, 6 ♀, 4 pupae, 14 larvae).

Asphondylia pilosa Gagné, New Species

Diagnosis.—This species and *clavata* are indistinguishable. Galls of the two species have the same general form except that that of *pilosa* has a thick covering of hair (Fig. 2e), while that of *clavata* is smooth (Fig. 2g). The two species are unique among the *auripila* group for the presence on the larva of four subequal anterior teeth on the spatula and three pairs of lateral papillae on each thoracic segment (Fig. 35). As with all the leaf galling asphondylias on *Larrea,* their ovipositors are among the shortest of the *auripila* group. The pupal antennal horn is shortened, the upper frontal horn is still wide enough to indicate a reduction from a bifid form, and the lower frontal horn is reduced.

Description.—*Adult:* Wing length: male, 2.6–3.0 mm (n = 5); female, 2.5–2.9 (n = 5). Labellum with 0–2 setae. Palpus with 3 segments, the first smallest with 0–2 setae, the second and third subequal in length with 2–5 setae laterally, the third tapering to the pointed apex. Ovipositor 1.0 times as long as seventh sternite (n = 3).

Pupa (Figs. 25, 26): Antennal horn short and tapered to rounded apex. Upper frontal horn short, simple, and wide. Lower frontal horn short, barely serrate.

Last instar larva: Spatula (as in Fig. 35) with 4 anterior teeth, the inner pair slightly shorter than the outer; area surrounding spatula sclerotized and pigmented. Three ventral papillae present on each side of thoracic segments, one singlet and one pair, the seta of the singlet longest.

Holotype.—Larva (one of two specimens under cover slip on slide, the specimen at right), from clavate, pilose gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-2-80, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-84 (7 ♂, 10 ♀, pupa, 7 larvae) and 8-15-85 (6 pupae, 1 larva); Parashant Canyon, river mile 198, Grand Canyon National Park, 4-3-1983 (3 pupae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (12 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-2-80 (3 pupae, 3 larvae), 8-29-80 (3 pupae, 3 larvae), 3-4-81 (3 larvae), and 8-31-83 (2 pupae, 2 larvae). BAJA CALIFORNIA: 3-4-89 (3 larvae).

Asphondylia resinosa Gagné, New Species

Diagnosis.—This species forms a short, leafy stem gall that is completely covered with hard, brown resin (Fig. 1g). This gall midge has several characters in common with *auripila* and *foliosa,* including the large size, the bifid upper frontal and trifid lower pupal horn, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. This is the largest species of the *auripila* group and differs from the two similar species in the elongate prothoracic spiracle that is abruptly bent anteriorly near the apex and in the shape of the spatula, which is rounded rather than angled laterally.

Description.—*Adult:* Wing length: male, 4.7 mm (n = 1); female, 4.5–4.9 mm (n = 7). Labellum with 0–1 setae. Palpus 3 segmented, the first small with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 2–6 setae laterally. Ovipositor 1.7 times as long as seventh sternite (n = 3), curved dorsally at tip.

Pupa (Figs. 14, 15): Antennal horns long, nearly rectangular in frontal view. Upper frontal horns bifurcate, lower frontal horn short, trifurcate, middle projection longer than the lateral projections. Prothoracic spiracles long, curved anteriorly at apex.

Last instar larva: Spatula (Fig. 36) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the outer; lateral edge of anterior margin of spatula curved

medially to join shaft; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of four specimens under cover slip on slide, the specimen at lower right), from solitary, foliaceous but resinous stem gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 12-4-1981, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 1-15-87 (19 pupae); Parashant Canyon, river mile 198, Grand Canyon National Park, 2-10-88 (♂, 4 ♀); Saguaro National Monument, East, 20 mi E Tucson, 2-25-80 (♂, 2 ♀, 2 pupae), 1-15-81 (4 pupae, 3 larvae); 1-15-83 (1 ♂, 6 ♀), 1-10-87 (♂, ♀, 18 pupae, 34 larvae); Tucson, 12-4-81, R. J. Gagné (4 larvae). TEXAS: El Paso, 3-23-51, J. A. Baker (pupa). MEXICO: Jalisco, 67-8948 (galls only).

Asphondylia rosetta Gagné, New Species

Diagnosis.—This species forms an elongate rosette gall on the stems (Fig. 1c). The spatula (Fig. 39) shows a resemblance to that of *A. apicata* and *A. florea*, but the pupal antennal horn is shorter and narrower than that of the other two species. The ovipositor of all three species is approximately of equal length, somewhat elongate for the *auripila* group.

Description.—*Adult:* Wing length: male, 3.0–3.1 mm (n = 2); female, 2.6–3.1 mm (n = 5). Labellum with 1–3 setae. Palpus 3 segmented, first smallest with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 3–5 setae laterally. Ovipositor 2.3 times longer than seventh sternite (n = 5), curved dorsally at tip.

Pupa (Figs. 16, 17): Antennal horns short, the apex broad in frontal view. Upper and lower frontal horns simple and long, about as long as antennal horns. Prothoracic spiracles short.

Last instar larva: Spatula (Fig. 39) with 2 rounded anterior teeth; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen at lower left), from elongate rosette gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (15 pupae, 7 larvae); Parashant Canyon, river mile 198, Grand Canyon National Park, 10-5-86 (3 ♂, 4 ♀, 33 pupae, 9 larvae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (2 pupae), 8-29-80 (♀, pupa, larva), 8-31-83 (20 pupae, 12 larvae), 9-15-84 (4 ♀, 4 pupae, 17 larvae), 4-15-87 (2 pupae). CALIFORNIA: Los Angeles (galls only).

Asphondylia silicula Gagné, New Species

Diagnosis.—This species forms a podlike, elongate, bilaterally flattened gall on the under surface of the leaf (Fig. 2d). The gall midge is similar to *fabalis*, except for a shorter pupal antennal horn. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, short antennal horn, and simple, large frontal horns. The spatula (Fig. 41) is blunt and slightly serrate anteriorly.

Description.—*Adult:* Wing length: male, 1.7 mm (n = 1); female, 1.6 mm (n = 1). Labellum with 3–5 setae. Palpus with one segment bearing 4–5 setae laterally. Ovipositor 1.0 times as long as seventh sternite (n = 3).

Pupa (Figs. 33, 34): Antennal horn long, broad and serrate anteromedially. Upper

and lower frontal horns simple, the lower smaller. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 44) with only indistinct serrations anteriorly; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen at lower right), from podlike leaf gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 3-15-87 (10 pupae, 2 larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (♀, 12 pupae), 3-1-81 (9 pupae, 8 larvae), 9-15-84 (3 pupae, 2 larvae), 3-15-87 (♂).

Asphondylia villosa Gagné, New Species

Diagnosis.—This species and *barbata* are indistinguishable, but their galls are distinctly different. Both are squat leaf galls with a rugose, hairless patch at the base. That of *villosa* is covered for almost its entire length with long hair (Fig. 1b), while that of *barbata* is covered for only slightly more than half its length with short hair. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long, wide, apically serrate antennal horn, and simple, large frontal horns. The spatula has two elongate teeth but is otherwise short.

Description.—*Adult:* Wing length: male, 1.6 (n = 1); female, 1.7–2.1 mm (n = 4). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.1 times as long as seventh sternite (n = 2).

Pupa (as in Fig. 22): Antennal horns long, flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, of approximately same length. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 42) with 2 prominent, long teeth almost as long as shaft; area surrounding spatula not modified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from hairy leaf gall on *Larrea tridentata,* Saguaro National Monument, East, 20 mi E Tucson, Arizona, 9-10-84, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-15-87 (♂, 2 ♀, 11 pupae, 6 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 9-1-86 (2 ♂, 2 ♀, 2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 9-10-84 (pupa, larva).

Discussion

More than 126 presumptive species of *Asphondylia* are known for the Nearctic Region and only 67 of them have been described, exclusive of this paper. Further, many of them are known only from adults, which are fairly homogenous in *Asphondylia.* The Nearctic species have not been revised since Felt (1916), when there were many fewer known. Nonetheless, because of recent studies of the *atriplicis* group (eight species that occur on Chenopodiaceae in California (Hawkins et al. 1986)), *A. websteri* (Gagné and Wuensche 1986), and an unpublished survey of certain characters on available stages of all known described Nearctic species, we are able to place the creosote bush species in context with the rest of *Asphondylia.*

The character matrix of Fig. 48 shows how the *auripila* group differs from other *Asphondylia* and how the species group can be further divided. The species on creosote bush share only one character state, the small adult labella with six or fewer setae and few,

scattered setulae on each (character 2). All creosote bush species have the larval lateral papillae reduced to two or three pairs (character 9), but the *atriplicis* group and *websteri* also have three pairs. Another character state, the single pair of terminal papillae (character 10), is shared by the *auripila* and *atriplicis* groups. Because these attributes result from losses, they could have evolved separately, so we are reluctant to propose a close relationship among the *auripila* and *atriplicis* groups and *websteri*. This is a common problem in determining relationships among species of *Cecidomyiidae* (Jones et al. 1983), but also among genera that share character states more indicative of life habits than of kinship (Sylvén 1975). Admittedly, the reductions within the *auripila* group could also have evolved independently more than once.

The *auripila* group sorts into three subgroups that fit well with their habits. These groups are the leaf, stem, and bud gall makers. The leaf gall makers of *Larrea*, namely *clavata, pilosa, digitata, discalis, fabalis, silicula, barbata,* and *villosa,* have in common the shortest ovipositor known in *Asphondylia*, the shaft being only about as long as the seventh sternite (character 4). The last six of these species share several losses or reductions, so differ somewhat from *clavata* and *pilosa*. The six are smaller (wing length 1.5–2.0 mm) than the medium-sized (2.1–3.1) *clavata* and *pilosa* (character 1), they have one- instead of three-segmented palpi (character 3), the larval spatula is greatly reduced in size and sclerotization (characters 7, 8), and they have lost a pair of lateral larval setae (character 9). The reduction of the adult palpus from three segments to one is unique within the *auripila* group, but the reduced larval spatula is also found in the bud gall makers. The loss of a lateral seta on each side of the spatula is shared by all the bud and stem gall makers.

The stem gall makers, *auripila, resinosa,* and *foliosa,* are large (wing length 3.2–4.9 mm) and females have a moderately long ovipositor, 1.4–1.7 times as long as the seventh sternite. Its three unique character states are the reduced medial lobes of the spatula (character 7) and the bifid upper (character 5) and trifid lower pupal frontal horns (character 6).

The bud gall makers, *apicata, bullata, florea,* and *rosetta,* are medium sized (wing length 2.1–3.1 mm), have the longest ovipositors of the *auripila* group (2.1–2.8 times as long as the seventh sternite), simple pupal frontal horns, and reduced spatulas and number of lateral papillae. The three last characters are common also to the leaf gall makers. As with the group of tiny leaf gall makers, *bullata* has lost the sclerotization surrounding the spatula (character 8).

Although our level of confidence that the *auripila* group is monophyletic could be greater, the evidence indicates that these species are the descendant of one founder species, which subsequently diverged onto the leaves, stems, and buds of *Larrea* before speciating further. We look forward to learning whether any *Asphondylia* spp. occur on other larreas in South America. If any do, they should shed light on the age and distribution not only of the *Asphondylia auripila* species group but also of its host.

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AN ASIAN ELM APHID (HOMOPTERA: APHIDIDAE) NEW TO NORTH AMERICA

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Abstract.—*Tinocallis saltans*, an Asian elm aphid, is reported for the first time in North America. It was first found in suction trap samples from Idaho, and subsequently in samples from Washington, Utah and Texas. It has also been collected from *Ulmus pumilla* in Idaho. Based on the sequence of dates of first collection at our various trapping locations, we think the aphid has been recently introduced.

Key Words: Aphididae, *Tinocallis saltans*, first report

A single specimen of a species of *Tinocallis* was found in a suction trap (Allison and Pike, 1988) sample at Parma, Canyon County, Idaho, in September, 1986. By using Remaudiere, Quednau and Heie (1988) and Zhang and Zhong (1983), we determined the aphid to be an Asian species, *Tinocallis saltans* (Nevsky) (Fig. 1). Our determination was confirmed by G. Remaudiere, and specimens matched those in the first author's possession from China determined by Zhang. Other species of *Tinocallis* reported in North America include *Tinocallis platani* (Kaltenbach), *T. ulmifolii* (Monell) and *T. nirecola* (Shinji) (Smith and Parron 1978, Kono 1983). Of these, the species found here most closely resembles *T. nirecola* but has much longer dorsal abdominal tubercles and oval (as opposed to linear) rhinaria on the third antennal segment.

In October, 1987, another ten specimens were collected in traps in Parma and Caldwell, both in Canyon County in southwestern Idaho. By 1988 the species was found consistently in trap samples in the warmer parts of the state, and it was collected for the first time in traps at cooler, higher elevations in southeastern Idaho. The first collection in northern Idaho (Lewiston) occurred in August, 1989. During May and June, 1989, it was the most abundant species in 4 out of 9 samples taken in Parma, indicating it has become well established in the warmest part of the state.

Tinocallis saltans has now been found in suction trap samples from the following locations (dates indicate year of first collection): Idaho—Aberdeen (1988), American Falls (1989), Caldwell (1987), Kimberly (1988), Lewiston (1989), Moscow (1989), Mountain Home (1988), Parma (1986), Preston (1989), Ririe (1988), Rockland (1989) and Soda Springs (1988); Oregon—Hermiston (1989); Texas—Amarillo (1989) and Lubbock (1989); Utah—Logan (1988), Salt Lake City (1988) and Vernal (1988); Washington—Connell (1989), Ephrata (1989), Paterson (1989), Prescott (1989), Prosser (1989) and Quincy (1989). No *T. saltans* specimens have been found in trap samples from the six trapping locations in

Fig. 1. *Tinocallis saltans* (Nevsky), collected from *Ulmus pumila*, Parma, ID, 27 September 1989.

Montana (Bozeman, Conrad, Huntley, Moccasin, St. Xavier and Sidney). Traps have been in place in Washington since 1984, in Idaho since 1985, in Montana and Utah since 1987, and in Texas only since 1989.

The collection sequence in Idaho appears to be typical for recently introduced aphid species. Examples include *Hyadaphis tataricae* (Aizenberg) and *Diuraphis noxia* (Mordvilko) (Voegtlin 1981, Stoetzel 1987, Halbert et al. 1986–1989). These species were also collected first in southwest Idaho, the warmest part of the state, and later at cooler locations. We think this pattern occurs because the longer, warmer season in southwest Idaho allows populations in this area to reach detectable levels first. Dates of first collection at new locations within a season reflect phenology rather than migration. Collections at new locations in subsequent years reflect range extension. Thus, based on the sequence of dates of first collection at each location, it is probable that *T. saltans* has also been recently introduced into North America. Because Idaho is an inland state without commerce involving importation of elm trees, it is unlikely the introduction occurred here.

Tinocallis saltans has been found on *Ulmus pumila* in Caldwell, Parma and Mountain Home, Idaho. *Ulmus americana* and *Ulmus parvifolia* were examined in Parma, but no *T. saltans* were found. In life, *T. saltans* has a bright, lemon yellow abdomen with dark markings. The thorax is dark brown. As the name suggests, the aphids jump readily.

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AN ANNOTATED LIST OF THE TRUE BUGS (HETEROPTERA) OF BERMUDA

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Abstract.—Listed from Bermuda are 45 species of Heteroptera, representing 14 families and 19 new island records. Only the mirid *Dagbertus bermudensis* Carvalho and Fontes is considered indigenous. All other species are thought to be adventive or introduced from eastern North America and the Caribbean Region. Available hosts and collection records for Bermuda, and general distribution are given for each species.

Key Words: arthropod fauna, inventory, Bermuda

This paper is part of a continuing series to inventory the arthropod fauna of Bermuda (Gordon and Hilburn 1989, Nakahara and Hilburn 1989a, b). Our purpose is to document the true bug fauna, to allow observations on faunal changes because of local extinction or future introductions, and to afford local biologists a means of recognizing potential pests and predators in conjunction with the included literature review and use of voucher specimens housed at the Bermuda Natural History Museum, Flatts.

Herein we report 45 species of Heteroptera from Bermuda, 19 of which are newly recorded. A number of previously recorded species have not been recollected in recent years, suggesting that they no longer occur on the islands. We were unable to confirm published records for the coreid *Euthoctha* sp., the pentatomid *Mormidea lugens* (Fabricius), and the scutellerid *Sphyrocoris obliquus* Germar. These unconfirmed reports and several new records, based on single or a few specimens, reflect the need for a continuing survey of the islands.

NATURAL HISTORY NOTES

Nakahara and Hilburn (1989a) reviewed the natural history of Bermuda, noting that because of its small size (54 sq. km/21 sq. mi.) and extreme isolation (1040 km/646 mi. from Cape Hatteras, North Carolina, USA), the fauna and flora are depauperate. Additionally, the aquatic insect life is limited to a few marine and brackish water species because there is no free-standing fresh water, except for temporary rain pools.

Prior to the present study, only 28 species of Heteroptera were reported from Bermuda. This figure can be compared with 166 species listed by Uhler (1894) from Grenada (133 sq. mi.; 344.5 sq. km), 126 species by Uhler (1893) from St. Vincent and Grenadines (150 sq. mi.; 388.5 sq. km), and 243 species by Van Duzee (1907) from Jamaica (4411 sq. mi.; 11,424.5 sq. km).

PAST WORK ON BERMUDIAN HETEROPTERA

Although numerous works treating the insects of Bermuda exist, relatively few have

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been devoted to Heteroptera. Kevan (1981), in his historical review of the terrestrial arthropods of Bermuda, discussed most of the early records of true bugs from 1603 through 1900. Uhler (1889) published the first list treating only Hemiptera (Heteroptera + Homoptera). Verrill (1902) added more insects, including 15 species of bugs. Van Duzee (1909) recorded nine species. Only a few other miscellaneous papers, treating mostly the applied aspects of Heteroptera, appeared until Ogilvie's (1928) "Preliminary Check List of the Insects of Bermuda." This paper, containing many host records and a listing of 28 species, has remained the most complete inventory of Bermudian bugs until the present study.

The Bermuda Department of Agriculture and Fisheries (BDAF) has maintained an insect collection since 1928. This collection is composed primarily of the L. Ogilvie (1928) material and later contributions by I. W. Hughes, Francis Monkman, and Kevin Monkman (Nakahara and Hilburn 1989a). Except for a small reference collection retained at the BDAF laboratory in Paget, this collection is now housed at the Bermuda Natural History Museum (BNHM) in Flatts.

Current Study

The following list includes all Heteroptera currently found in the BNHM collection, those reported in the literature, and specimens collected by M. R. Wilson, CAB International Institute of Entomology, London (July 1988) and us (Hilburn, 1987–1988; Henry, Jan. 1988). All specimens were identified by the senior author, except the Cydnidae by R. C. Froeschner.

The heteropteran fauna of Bermuda is represented by 14 families as follows: Anthocoridae (4 spp.), Berytidae (1 sp.), Cimicidae (1 sp.), Coreidae (2 spp.), Corixidae (1 sp.), Cydnidae (2 spp.), Gerridae (1 sp.), Lygaeidae (9 spp.), Miridae (11 spp.), Nabidae (1 sp.), Pentatomidae (6 spp.), Reduviidae (2 spp.), Rhopalidae (2 spp.), and Scutelleridae (2 spp.). Only the mirid *Dagbertus bermudensis* Carvalho and Fontes is considered indigenous to Bermuda.

Although 28 species have been reported, several of these records are based on misidentifications or are synonyms. Therefore, despite the discovery of 19 previously unreported bugs, the 45 species reported here is only an increase of 17 over the 28 listed by Ogilvie (1928).

Names in this paper are arranged alphabetically by family, subfamily, tribe, genus, and species, followed by a list of literature mentioning Bermudian Heteroptera, the parishes (Fig. 1) where the respective bugs have been found, the month collected, a summary and reference to food plants and habits when known, and general distribution. Voucher material is housed in the collection of the Bermuda Natural History Museum, Flatts, the British Museum (Natural History), London, and the United States National Museum of Natural History, Washington, D.C.

Because Bermuda shares much of its fauna with that of eastern United States, Blatchley's (1926) "Heteroptera of Eastern North America" is one of the most useful references to consult for species recognition. Even though many of his names are outdated, their current status can be checked in the Henry and Froeschner (1988) Heteroptera Catalog. For more recent revisionary works containing keys and other information not cited in the above Heteroptera catalog, see the references listed under the respective taxa in the text.

Heteroptera of Bermuda

Family Anthocoridae

Subfamily Anthocorinae

Montandoniola moraguezi (Puton). Cock 1985: 120.

Parish records: Paget, St. George's (June–July).

This species was introduced into Bermuda in mid-1973 from specimens collect-

Fig. 1. Parish map of Bermuda (after Jones 1979).

ed in Hawaii to control the laurel thrips, *Gynaikothrips ficorum* (Marchal). Cock (1985) reported it well established by the end of 1973. Specimens collected in 1988 were found on *Petunia* sp. [Solanaceae]. It is widely distributed in the South Pacific islands and Hawaii. It also has been introduced into California (USA) and Canada but is not known to be established.

Orius insidiosus (Say) [insidious pirate bug]. Ogilvie 1928: 19.

Paris records: Devonshire, Paget, Sandys, Smith's, St. George's (Jan., Apr., July–Sept.).

This well-known species is a predator of small arthropods and has been the subject of numerous economic studies. Common on many plants throughout Bermuda, it is widespread from North to South America, and in the West Indies.

Subfamily Lasiochilinae

Lasiochilus fraternus Uhler. NEW RECORD.

Parish records: Paget, Smith's (Jan.).

In Bermuda, single males were beaten from the shrub *Raphiolepis indica* (L.) Lindley [Rosaceae] and an *Ipomoea* sp. [Convolulaceae]. Previously *L. fraternus* was known only from Grenada based on the original description (Uhler 1894).

Subfamily Lyctocorinae

Xylocoris galactinus Fieber. NEW RECORD.

Parish record: Paget (Jan.).

In Bermuda, a single specimen was collected along Berry Hill Road, Paget. This widespread predatory species is found throughout Europe and North America, most often in stored grains and compost piles and under dead bark.

Family Berytidae

Subfamily Metacanthinae

Metacanthus tenellus Stål. NEW RECORD.

Parish records: Smith's (Jan., Nov.).

In Bermuda, adults and nymphs were abundant at Spittal Pond on *Acalypha alopecurioides* Jacq. [Euphorbiaceae]. This species is known from South America north to Florida and Texas in the United States, and the West Indies.

Family Cimicidae

Cimex lectularius Linnaeus [human bedbug]. Verrill 1902: 386; Ogilvie 1928: 19.

Parish records: No Bermuda specimens examined.

This cosmopolitan species is found in all areas of human habitation.

Family Coreidae

Subfamily Coreinae

Anasa scorbutica (Fabricius). Ogilvie 1928: 18.

Parish records: Paget (Apr., June).

No Bermuda specimens have been collected since 1925. This species is a cucurbit specialist, known from the southern United States to South America, and the West Indies.

Euthoctha galeator (Fabricius). Ogilvie 1928: 18 (as *Euthoctha* sp.).

Parish records: No Bermuda specimens examined.

Ogilvie's (1928) record of "*Euthoctha* sp." may represent a misidentification; however, none of his material was found to allow us to verify this speculation. *Euthoctha galeator* is widespread in the United States from New England to Wisconsin, south to Florida and Texas.

Family Corixidae

Trichocorixa reticulata (Guérin-Méneville). Hughes and Schuster 1986: 387.

Parish records: Paget, Smith's, Warwick (Mar., July, Oct.).

This species is said to be very common in brackish ponds and tide-wash pools and is often taken in light traps. It is widespread from Florida to California in the United States to South America, and in the West Indies, China, Hawaii, and many of the Pacific Islands.

Family Cydnidae

Subfamily Cydninae

Pangaeus bilineatus (Say). Uhler 1889: 463; Verrill 1902: 388; Ogilvie 1928: 17; Sailer 1954: 43; Froeschner 1960: 463.

Parish records: Paget, Pembroke, Southampton, St. George's (Mar.–Apr., June–July).

This cydnid is commonly taken in light traps and is said to be injurious to strawberries (Ogilvie 1928). It is widespread from the United States to Guatemala (Froeschner 1960).

Rhytidoporus indentatus Uhler. NEW RECORD.

Parish records: Paget, Southampton, St. George's (July, Oct.).

All Bermuda specimens of *R. indentatus* were taken at lights. Although Ogilvie's (1928: 17) specimens apparently are lost, his record of *Aethus* sp., the only other cydnid he listed from Bermuda, probably refers to this species. Previously known only from the West Indies and Florida in the United States (Froeschner 1960).

Family Gerridae

Subfamily Halobatinae

Halobates micans (Eschscholtz). Ogilvie 1928: 18 (as *H. wullerstorfi* [*sic*], a junior synonym of *H. micans*); Hughes and Schuster 1986: 388.

Parish records: Devonshire, St. George's (June–July).

Bermuda specimens of *H. micans* were taken in a saltwater pool and on south shore beaches. This open-ocean species, widespread in all tropical seas, is distributed in the Atlantic as far north as North Carolina.

Family Lygaeidae

Subfamily Blissinae

Blissus insularis Barber [southern chinch bug]. NEW RECORD.

Parish records: Devonshire, Hamilton, Paget (June–Aug., Oct.).

The first Bermuda specimens of this species were taken in 1979. This severe pest of St. Augustinegrass, *Stenotaphrum secundatum* (Walt.) Ktze. [Poaceae], is widespread in the southern United States, Mexico, and the West Indies.

Subfamily Cyminae

Cymodema breviceps (Stål). NEW RECORD.

Parish record: Paget (July).

This species is most often swept from grasses and sedges. It is widespread from New York to Florida, west to California in the United States, and south through Mexico to Argentina, and in the West Indies.

Cymoninus notabilis (Distant). Scudder 1957: 105; Slater 1964: 423; Brailovsky 1975: 177; Ashlock and Slater 1988: 188.

Parish record: Paget (July).

This lygaeid is widespread from Florida to Texas in the United States to South America, and in the West Indies.

Subfamily Geocorinae

Geocoris punctipes (Say). NEW RECORD.

Parish record: Sandys (Aug.).

This largely predatory species is widespread from the southern United States to Colombia. Only two specimens have been taken in Bermuda, both at Hog Bay Level in 1987.

Subfamily Orsillinae

Nysius scutellatus Dallas. NEW RECORD.

Parish records: Devonshire, Paget, Sandys (Jan., Sept.–Oct., Dec.).

This species previously was recorded as *N. ericae* (Schilling) and *Nysius* sp. by Ogilvie (1928: 18). Barber's (1939: 342) record probably also applies to *N. scutellatus*. We collected this lygaeid on the fruits of *Euphorbia hirta* L. [Euphorbiaceae] at the Botanical Gardens. We note that the genus *Nysius* is in great need of revision and recommend that Bermudian material eventually be reexamined. *Nysius scutellatus* is known from Virginia to Florida in the United States, and the West Indies.

Subfamily Rhyparochrominae

Neopamera bilobata (Say). Van Duzee 1909: 127 (as *Pamera bilobata*), Ogilvie 1928: 18 (as *Pamera bilobata*).

Parish records: Hamilton, Paget, Smith's, Sandys, St. George's (Jan., June, Aug.–Nov.).

This species has been reported in Bermuda on heads of *Chaetochloa* spp. [Poaceae] (Ogilvie 1928). It is widespread from the southern United States to Argentina, and the West Indies.

Ozophora divaricata Barber. NEW RECORD.

Parish records: Devonshire, Smith's (Feb., June–July).

Seven specimens of *O. divaricata* were taken at the Arboretum on *Hibiscus* sp. [Malvaceae]. It previously has been recorded from the Bahamas, the Greater Antilles, and Florida (USA) (Slater and Baranowski 1983).

Paromius longulus (Dallas). Ogilvie 1928: 18 (as *Pamera longula*).

Parish records: Devonshire, Paget, Sandys, Smith's, Southampton, St. George's (Jan.–Feb., Apr., June–Oct.).

This grass-feeding lygaeid has been reported in Bermuda on heads of *Chaetochloa* spp. [Poaceae] (Ogilvie 1928). It is frequently collected by sweeping and is widespread from the United States to South America, and the West Indies.

Pseudopachybrachius vinctus (Say). NEW RECORD.

Parish records: Devonshire, Hamilton, Paget, Pembroke, Sandys, Smith's, St. George's (June–Oct.).

The first specimens of this species were collected at Trott's Pond in 1966. It is widespread from the United States to South America, and the West Indies.

Family Miridae

Subfamily Bryocorinae

Tribe Dicyphini

Cyrtopeltis modesta (Distant). NEW RECORD.

Parish records: Devonshire, Paget, Sandys (Jan., July).

This species, sometimes called the "tobacco suckfly," has been recorded as a tobacco and truck crop pest, but also may be partially predatory. In 1988 one adult and one nymph were taken at the Botanical Gardens on *Dombeya* sp. [Sterculiaceae]. It later was found in abundance on tomato in July. This mirid is widespread from southern United States to South America, and in the West Indies.

Subfamily Mirinae

Tribe Mirini

Dagbertus bermudensis Carvalho and Fontes 1983: 160.

Parish records: Devonshire, Paget, Sandys, Smith's, Southampton (Jan., June–July).

This mirid was reported by Parker (1945: 3) as "the tarnished plant bug or an insect closely resembling the tarnished plant bug. . . ." Records of *Lygus olivaceus* Reuter by Van Duzee (1909: 127), Ogilvie (1928: 19), and Carvalho (1959: 80) and those of *Dagbertus hospitus* (Distant) by Kelton (1974: 378) should be referred to the greenish females of *D. bermudensis*. Van Duzee's (1909: 127) mention of a strongly marked *Lygus* sp. certainly refers to the darker, sexually dimorphic, males of this species. This plant bug is a cupressaceous specialist, apparently preferring *Juniperus bermudiana* L., but adults and nymphs also were commonly found throughout Bermuda on ornamental *Cupressus, Juniperus,* and *Thuja* spp. *Dagbertus bermudensis* is the only indigenous heteropteran known from Bermuda.

Lygus lineolaris (Palisot) [tarnished plant bug]. Van Duzee 1909: 127 (as *Lygus pratensis* L.); Ogilvie 1928: 19 (as *L. pratensis*).

Parish records: Devonshire, Hamilton, Paget, Sandys, Smith's, Southampton, St. George's (Jan., May–July, Sept.–Dec.).

Ogilvie (1928) reported this species frequent in Bermuda, causing severe damage to broad beans. It has been recorded as a pest of many plants, including cotton, forage, and many food crops. All reports of *Lygus pratensis* in Bermuda should be referred to *L. lineolaris*. *Lygus lineolaris* is widespread from Canada to northern Mexico.

Taylorilygus pallidulus (Blanchard). Van Duzee 1909: 127 (as *Lygus apicalis* var. *prasinus* Reuter); Ogilvie 1928: 19 (as *Lygus apicalis* var. *prasinus, Lygus pabulinus* L., and *Lygus godmani* Distant); Carvalho 1959: 265.

Parish records: Paget, Sandys, Smith's, St. George's (Jan., July, Sept.–Dec.).

Study of Ogilvie's (1928) determined material indicates that all of the species listed above actually are misidentifications of *T. pallidulus*. This species has numerous hosts, mostly in the Asteraceae. In Bermuda, adults and nymphs were common on *Conyza canadensis* (L.) Cronq. [Asteraceae]. It is widespread in the Old World, North to South America, and the West Indies, and is considered nearly cosmopolitan.

Tribe Stenodemini

Dolichomiris linearis (Reuter). NEW RECORD.

Parish record: Sandys (Nov.).

The only specimen known from Bermuda was collected in 1987. This species, most often swept from coastal grasses and sedges, is widespread in the Old World. In the New World it is recorded from Florida and Texas in the United States to South America, and the West Indies.

Trigonotylus tenuis Reuter. Verrill 1902: 387 (as *Trigonotylus ruficornis* (Geoffroy)); Ogilvie 1928: 19 (as *T. brevipes* (Jakovlev)); Kelton 1971: 699 (as *T. dohertyi* (Distant)).

Parish records: Devonshire, Hamilton, Paget, Pembroke, Sandys, Smith's, Southampton, St. George's (Jan., Mar., July–Dec.).

The primary host of this plant bug is bermudagrass, *Cynodon dactylon* (L.) Pers. [Poaceae]. It is widespread in all warmer parts of the world and common from southern United States to South America, and the West Indies. We follow Golub's (1989) treatment of *T. doddi* (Distant) as a junior synonym of *T. tenuis*.

Subfamily Orthotylinae

Tribe Halticini

Halticus bractatus (Say) [garden fleahop-

per]. Waterston 1940: 4 (as *Halticus citri* Reuter).

Parish records: Devonshire, Hamilton, Paget, Sandys, Smith's (Jan., Apr., June–Aug., Oct.–Dec.).

The garden fleahopper is often a serious pest of truck crops. In Bermuda, it has been recorded from celery, cucumber, egg plant, pumpkin, soybean, squash, sweetpotato, and tomato (Waterston 1940). This tiny, often brachypterous, species frequently is mistaken for black flea beetles (Coleoptera: Chrysomelidae). It is widespread from North to South America, and Hawaii and the West Indies.

Subfamily Phylinae

Tribe Leucophoropterini

Tytthus parviceps (Reuter). NEW RECORD.

Parish records: Devonshire, Paget, Sandys (Jan., July).

This species is probably predatory on homopteran eggs in grasses, where it is most often collected. It is widespread in Africa, the Mediterranean Region, the West Indies, and from Florida (USA) to Panama.

Tribe Phylini

Rhinacloa clavicornis (Reuter). Schuh and Schwartz 1985: 400.

Parish records: Devonshire, Paget, St. George's, Sandys, Smith's (Jan., July).

In Bermuda, *R. clavicornis* was swept from various Asteraceae in old fields. It is widespread from the southern United States to South America, and in the West Indies (Schuh and Schwartz 1985).

Spanagonicus albofasciatus (Reuter) [white-marked fleahopper]. Ogilvie 1928: 19 (as *Leucopoecila albofasciata*).

Parish records: Devonshire, Paget, Sandys (May, July).

This small species has numerous hosts, but favors Fabaceae, and is often destructive to clovers in lawns. It is widespread from North to South America, and in the West Indies.

Tribe Pilophorini

Sthenaridea vulgaris (Distant). NEW RECORD.

Parish records: Devonshire, Paget, Sandys, Smith's (Jan., June–July, Oct.–Nov.).

In Bermuda, *S. vulgaris* was collected at light traps and by sweeping grasses and sedges. This species, recorded from *Cyperus luzulae* Rotth. [Cyperaceae], is widespread from Florida and Texas (USA), the Caribbean Region, and Mexico to southern Brazil (Schuh and Schwartz 1988).

Family Nabidae

Nabis capsiformis Germar. Van Duzee 1909: 127; Ogilvie 1928: 18; Harris 1939: 376.

Parish records: Sandys, Smith's, Southampton, St. George's, Warwick (Jan.–Feb., June–July, Oct.–Nov.).

This nabid preys on coexisting arthropods. It is known from the southern United States to South America, the West Indies, and warmer areas of the Old World.

Family Pentatomidae

Subfamily Asopinae

Podisus maculiventris Uhler [spined soldier bug]. NEW RECORD.

Parish records: Devonshire, Pembroke, Smith's (Jan., Mar., July–Aug., Nov.).

Although never reported, the first Bermuda specimens of this species were collected in 1944. This stink bug is predaceous on lepidopterous larvae, Coleoptera, and other arthropods. It is widespread in North America and has been introduced into Europe and Korea for biological control.

Subfamily Pentatominae

Banasa euchlora Stål [cedar bug, cedar berry bug, green bug]. Verrill 1902: 386; Ogilvie 1928: 17; Parker 1945: 3.

Parish records: Devonshire, Hamilton,

Paget, Sandys, Southampton, Warwick (Jan.–Mar., June).

This stink bug is known to feed on the fruits of *Juniperus* spp. [Cupressaceae]. It is widespread in North America from Maryland, Iowa, and Colorado, to Florida, Arizona, and northern Mexico. Kevan's (1981) tentative referral of an early "greenbug" record to *Nezara viridula* (L.) probably should be applied to this species.

Banasa herbacea (Stål). NEW RECORD.

Parish records: Hamilton, Sandys (Jan., Mar.).

Two Bermuda specimens of this green stink bug were collected at Ft. Scaur in 1987 and 1988 on *Juniperus bermudiana* L. [Cupressaceae]. It is known from the West Indies and southern Florida in the United States.

Mormidea lugens (Fabricius). Verrill 1902: 387; Van Duzee 1909: 127; Ogilvie 1928: 18; McPherson 1982: 54.

Parish records: No Bermuda specimens examined.

This species is primarily a grass feeder, but there are records of adults swarming over numerous other plants (McPherson 1982). Verrill (1902) reported *M. lugens* as injurious to tomatoes and beans in Bermuda. It is known from Quebec to Wyoming in the United States to Mexico, and the West Indies.

Murgantia histrionica (Hahn). [harlequin bug]. Bennett and Hughes 1959: 429; Cock 1985: 134.

Parish records: Paget, Pembroke, Sandys, Southampton, St. George's (Feb., July, Sept., Nov.–Dec.).

This colorful species is often a serious pest of Brassicaceae (cabbage and other cole crops) (McPherson 1982), but it occurs sporadically in Bermuda and is usually of minor importance. It is widespread in North America south to Mexico and Central America and has been accidentally introduced into Hawaii.

Nezara viridula (Linnaeus) [southern green stinkbug]. Verrill 1902: 386; Uhler 1889: 154; Van Duzee 1909: 127 (also as *Nezara* sp. based on unusual nymphs); Ogilvie 1928: 18.

Parish records: Devonshire, Paget, Pembroke, Smith's, St. George's (Jan.–Apr., July–Aug., Oct., Dec.).

This stink bug is an occasional pest of soybeans and numerous truck and fruit crops. Widespread throughout the warmer parts of the world, it is recorded from the southern United States to South America, the West Indies, and the Afrotropical, Australian, Oriental, and Palearctic Regions.

Family Reduviidae

Subfamily Emesinae

Empicoris rubromaculatus (Blackburn). NEW RECORD.

Parish records: Devonshire, Paget, Sandys, Smith's (June, Jan.).

In Bermuda, this small, slender predatory species was taken on *Nerium oleander* L. (oleander) [Apocynaceae], *Pittosporum* sp. [Pittosporaceae], and beaten from a thick hedge of *Viburnum suspensum* Lindl. [Caprifoliaceae]. The first Bermuda specimens were collected in 1987. It is common across the southern United States and is recorded as far north as British Columbia. This species considered nearly cosmopolitan.

Subfamily Harpactorinae

Zelus longipes (Linnaeus). NEW RECORD.

Parish records: Hamilton, Paget, Pembroke, Sandys, Smith's (Jan., Mar., Aug., Oct.–Nov.).

This black and orange predatory species was first collected in 1979 and is now common in many areas of Bermuda. It ranges from Florida to California in the United States to South America, and in the West Indies.

Family Rhopalidae

Harmostes serratus (Fabricius). NEW RECORD.

Parish records: Hamilton, Pembroke, Smith's, St. George's (Jan., June–Oct., Dec.).

Although not previously reported, this was first collected in Bermuda at Trott's Pond in 1966. It is known from Florida and Texas in the United States to South America, and the West Indies.

Liorhyssus hyalinus (Fabricius). Verrill 1902: 387 (as *Corizus hyalinus*); Hambleton (1908: 136); Van Duzee (1909: 127, as *Corizus hyalinus*); Barber 1923: 22 (as *Corizus hyalinus*); Ogilvie 1928: 18.

Parish records: Paget, Sandys, Smith's, Southampton (Jan., June–Dec.).

In Bermuda this nearly cosmopolitan species was taken on "*Ruellia squarrosa*" [as labeled in the Botanical Gardens] [Acanthaceae] and fruits of *Euphorbia hirta* L. [Euphorbiaceae] at the Botanical Gardens. It is also frequently taken by sweeping mixed vegetation. This rhopalid is widespread from North to South America, and the West Indies and is also recorded from Africa, Asia, Australia, Hawaii, and Europe.

Family Scutelleridae

Sphyrocoris obliquus Germar. Ogilvie 1928: 18.

Parish records: No Bermuda specimens examined.

This shield bug is known from Florida to California in the United States, south to Colombia, and the West Indies.

Stethaulax marmoratus (Say). Ogilvie 1928: 18.

Parish records: Paget (Nov.–Dec.).

This species has not been collected in Bermuda since 1924. It is recorded feeding on *Juniperus* sp., *Thuja occidentalis* L. [Cupressaceae], and numerous other trees and shrubs, and has been reared on *Rhus glabra* L. [Anacardiaceae] (McPherson 1982). It is known from New York to Oregon, south to Florida and California.

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SCANNING ELECTRON MICROSCOPY OF THE EGGS OF *AEDES VEXANS* AND *AEDES INFIRMATUS* (DIPTERA: CULICIDAE)

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Abstract.—Descriptions based on scanning electron micrographs are given of the eggs of *Aedes* (*Aedimorphus*) *vexans* (Meigen) and *Ae.* (*Ochlerotatus*) *infirmatus* Dyar and Knab. The intact surface detail of the eggs is shown, including the dorsal, lateral and ventral surfaces, and the posterior pole, anterior pole and micropyle. This is in contrast to earlier descriptions which were incomplete and which were based on eggs from which the outer chorion was removed.

Key Words: Insecta, mosquito, egg, fine structure, chorionic sculpturing, scanning electron microscopy

The eggs of *Aedes* (*Aedimorphus*) *vexans* (Meigen) and *Ae.* (*Ochlerotatus*) *infirmatus* Dyar and Knab were first described, respectively, by Horsfall and Craig (1956) and Craig and Horsfall (1960). The descriptions were augmented by phase contrast photomicrographs of the chorionic sculpturing after preparative methods (Craig 1955) that removed the outer chorion. In the case of *Ae. vexans,* material prepared in the same way was examined also by Myers (1967) and Kalpage and Brust (1968) to provide additional illustrations based on phase contrast microscopy. As the scanning electron microscope came into more general use, Horsfall et al. (1970) re-examined the egg of *Ae. vexans* and other species and published a number of electron micrographs showing several variants, including details of the chorionic sculpturing and micropyle. Again, however, the outer chorion was removed prior to examination, so that the micrographs do not show the structure of the intact egg. None of these earlier illustrations, either of *Ae. vexans, Ae. infirmatus,* or other species examined, show the intact outer chorion and real appearance of the eggs.

Despite the fact that structures of the outer chorion may not appear taxonomically useful under light microscopy (Myers 1967), they incorporate a potential for interspecific variation not found in the inner chorionic sculpturing, the simple reticulate outline created by the chorionic cell boundaries. Scanning electron microscopy, a technique now readily available to most workers, was used in this paper to provide more complete and quantitative descriptions of the intact eggs of *Ae. vexans* and *Ae. infirmatus,* including details of the anterior pole and micropyle, the posterior pole, and differences between the dorsal and ventral surfaces of the egg.

MATERIALS AND METHODS

Females of *Ae. vexans* were collected by aspiration in citrus groves within 8 km of the Florida Medical Entomology Laboratory, while *Ae. infirmatus* females were collected on the laboratory grounds. About 15

females of each species were allowed to take blood to repletion from the author's arm and were then enclosed individually in 2.5 × 4.0 cm cylindrical containers placed on damp cheese-cloth several layers thick. In a few days most females had laid some eggs, which were washed carefully into a single small dish with filtered distilled water. The eggs were then thoroughly mixed and pipetted onto small (<15 mm) circles of filter paper. The specimens were kept covered and allowed to embryonate fully, and were then dried first in air, then in a desiccator over calcium chloride for 24 h. The filter paper circles were fixed to stubs with silver paint and, 24 h later, coated with gold. Specimens were examined in a Hitachi S-510 scanning electron microscope.

The terminology follows Harbach and Knight (1980), except for the terms anterior ring and outer chorionic cell field, which are defined by Linley (1989).

Results

Aedes (*Aedimorphus*) *vexans* (Figs. 1–3)

Size: dimensions as in Table 1.

Color: dark bronze.

Overall appearance: shape variable, curvature of ventral surface greater than dorsal, greatest diameter somewhat anterior to middle, anterior taper more pronounced, posterior more gradual (Fig. 1). Outer chorionic cells uniformly elongate longitudinally (in long axis of egg), each more or less completely filled by longitudinally aligned outer chorionic tubercles. Tubercles occasionally in a single row, but usually in two rows, at least at widest part of cell. Micropylar collar indistinct.

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 1). Outer chorionic cells longitudinally elongate, 20–42 μm long, 8–12 μm wide (2.5–5 times as long as wide), irregularly polygonal with boundaries clearly defined but not very straight (Figs. 1, 2a, b). Cell fields 17–39 μm

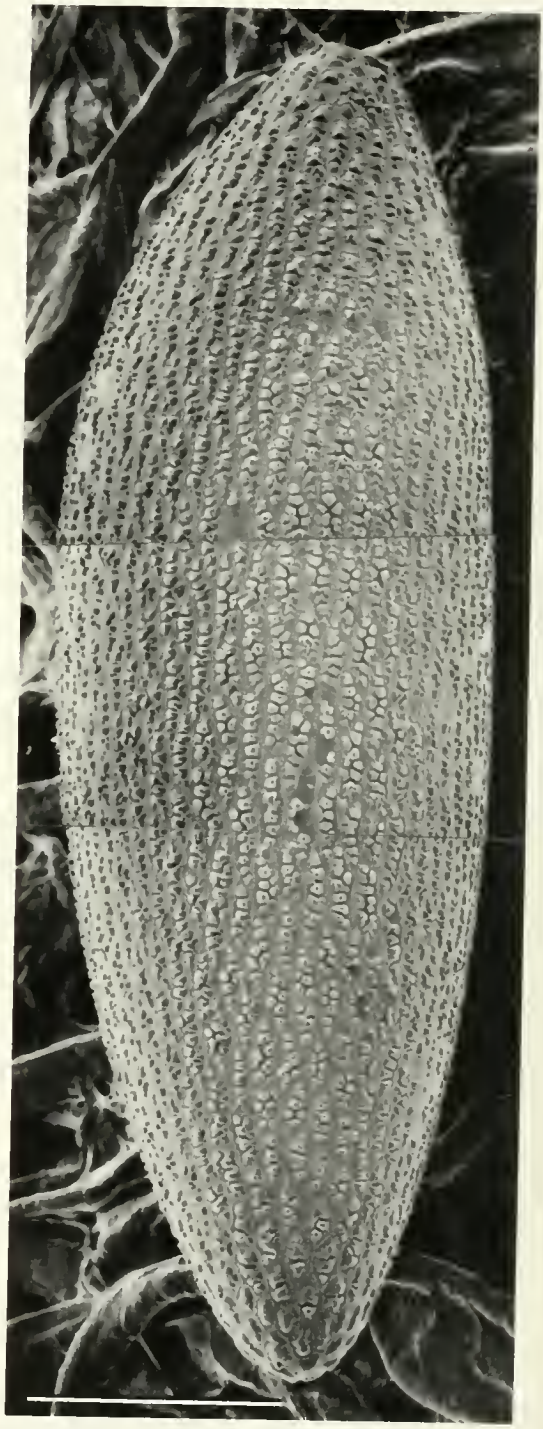


Fig. 1. *Ae. vexans.* Entire egg lateral view; dorsal surface at right, anterior end at top. Scale = 100 μm.

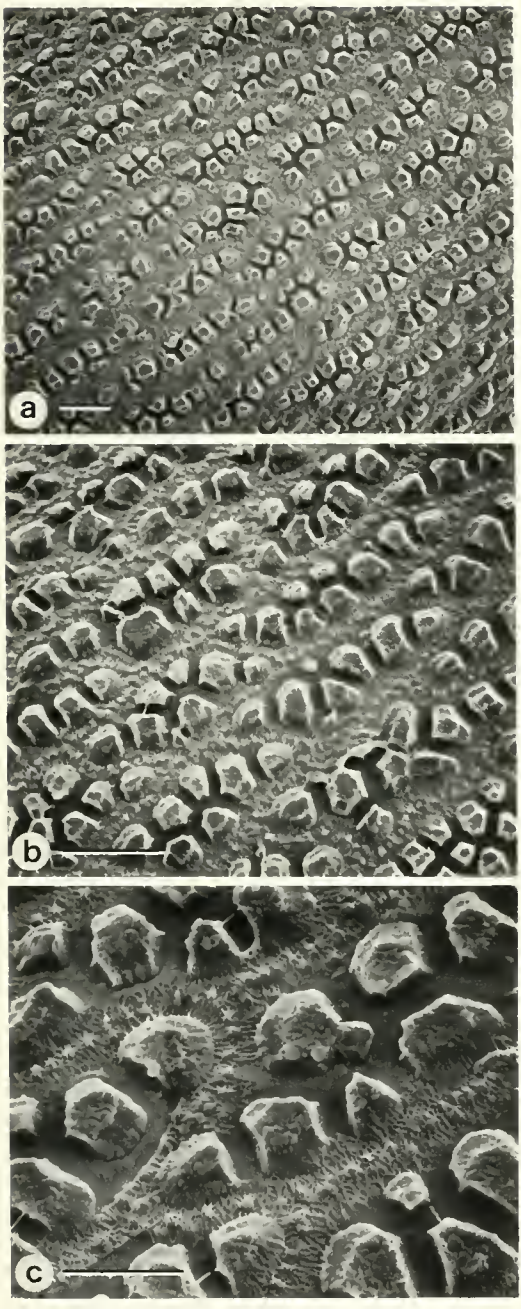


Fig. 2. *Ae. vexans.* (a) Outer chorionic cells, ventral surface, middle of egg; (b) detail of outer chorionic cells and tubercles; (c) detail of individual outer chorionic tubercles and outer chorionic reticulum. Scale = 10 μm (a, b), = 5 μm (c).

long, 7–10 μm wide, with smooth floors (Fig. 2c). Outer chorionic tubercles 6–15 in number, fewer per cell on dorsal surface than on ventral (lateral surface not counted), but not significantly so (Table 2). Tubercles arranged longitudinally in a single row, or more frequently a double row at widest parts of cell (Fig. 2a, b). Outer edges of tubercles almost always touching outer chorionic reticulum, gaps separating tubercles strikingly uniform, ca. 1.5 μm (Fig. 2a, b).

Shape of tubercles irregular, roughly polygonal, shapes of edges tending to match those of adjacent tubercles (Fig. 2b), largest tubercles ca. 5.5 μm in longest dimension, smallest ca 2.4 μm, but very small tubercles uncommon. In detailed structure, each tubercle consists of a base, often with slightly concave inner edges with sloped, tapered walls rising to a smaller, flat top ornamented with poorly defined bumps and fissures (Fig. 2b, c). Outer edges of tubercle bases usually rounded (Fig. 2c). Outer chorionic reticulum low, width 1.2–3.5 μm, consisting of a very fine reticulate meshwork with central line of small, bead-like protuberances (Fig. 2b, c), more or less evenly spaced (1.0–3.2 μm). Meshwork usually touching and continuing some distance up sides of tubercles (Fig. 2c).

Anterior pole and micropyle: outer chorionic cells diminish somewhat in length towards anterior pole, becoming narrower, with outer chorionic cells reduced to single row (Fig. 3a, b). Tubercles not all separated by uniform gaps (Fig. 3a), many gaps narrower and shallow. Many tubercles close together or almost fused, appearing more rounded and less distinct, especially just posterior to micropyle (Fig. 3b). Anterior ring present but not well formed, usually incomplete (Fig. 3c, d), diameter 35–45 μm, variable, and of very variable width (0–7 μm). Micropylar collar not prominent (Fig. 3a), height 6–10 μm and variable, diameter 20–28 μm and not always circular or continuous (Fig. 3c, d), internal diameter 18–23 μm, wall width 2–6 μm, very variable,

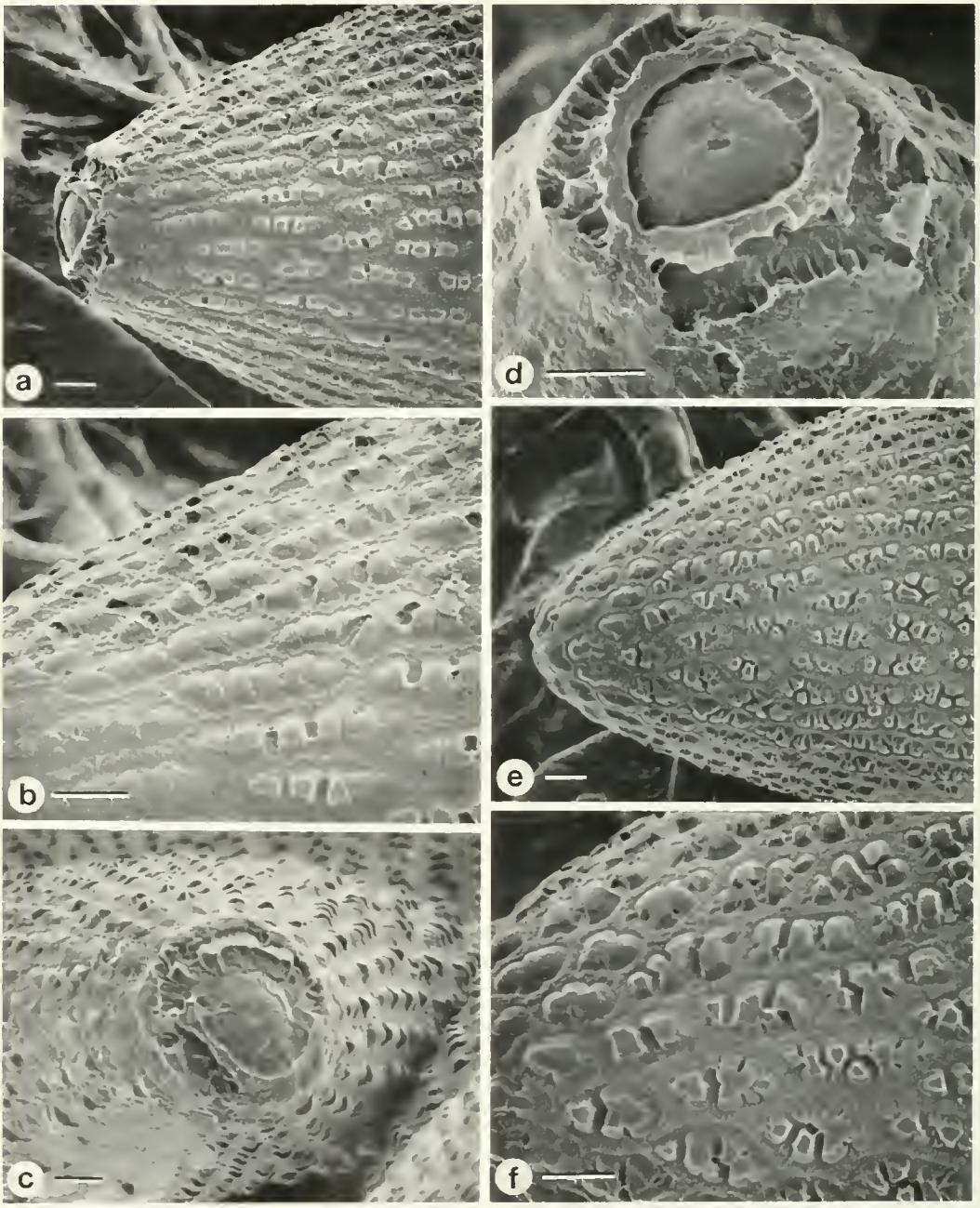


Fig. 3. *Ae. vexans.* (a) Anterior pole and micropylar apparatus, lateral surface; (b) anterior pole, lateral surface, chorionic cell detail; (c) top view, anterior pole and micropylar apparatus; (d) top view, detail of micropylar apparatus; (e) posterior pole, lateral surface; (f) posterior pole, ventral surface, outer chorionic cell detail. Scale = 10 μm.

Table 1. Dimensions of the eggs of two species of *Aedes* (n = 15).

Species	Length (μm)		Width (μm)		L/W Ratio	
	Mean (±SE)	Range	Mean (±SE)	Range	Mean (±SE)	Range
Ae. vexans	650.9 ± 3.3	637.3–665.3	197.6 ± 1.8	193.7–203.9	3.29 ± 0.03	3.14–3.54
Ae. infirmatus	664.4 ± 3.6	637.3–685.7	207.8 ± 1.9	201.4–224.3	3.20 ± 0.03	3.02–3.40

outer margin irregular. Micropylar disc fairly clearly defined, domed (Fig. 3c, d), diameter 10–18 μm, micropyle indistinctly trilobed, diameter ca. 2.6 μm.

Posterior pole: outer chorionic cells become shorter near posterior pole, gaps between outer chorionic tubercles become more irregular (Fig. 3e), some tubercles fused and all fused in cells immediately at and adjacent to pole (Fig. 3e, f).

Aedes (*Ochlerotatus*) *infirmatus* (Figs. 4–6)

Size: dimensions as in Table 1.

Color: satiny black.

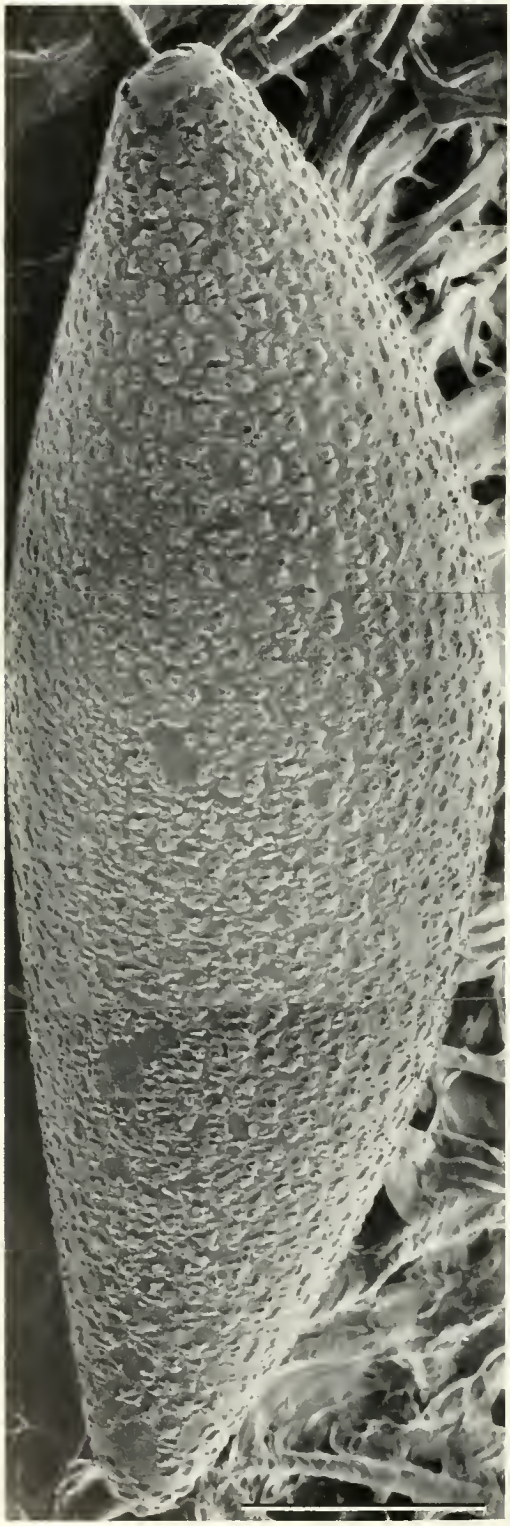
Overall appearance: shape fusiform, somewhat variable, ventral surface more convex than dorsal, widest point just anterior to middle, anterior taper more abrupt than posterior, both anterior and posterior dorsal margins straighter than more curved ventral margins (Fig. 4). Outer chorionic cells appearing irregular in outline, boundaries difficult to distinguish, outer chorionic tubercles clearly visible and many quite large, but not conforming to any easily discernible pattern (Fig. 4). Micropylar collar relatively inconspicuous, conforming to taper of egg.

Chorion, ventral surface: outer chorionic cells somewhat longitudinally elongate, polygonal, but very variable in form, 20–26 μm long, 10–13 μm wide, boundaries quite straight (Fig. 5a), corresponding cell field dimensions ca. 17–25 μm and 9–11 μm. Outer chorionic tubercles 2–7 in number, fewer than on lateral and dorsal surfaces (Table 2), more or less evenly spaced longitudinally in cell, usually but not always touching outer chorionic reticulum on at least one side (Fig. 5a, d). Largest tubercles 6–11 μm long (longest dimension), some as small as 1.2 μm, but very small tubercles fairly uncommon. Form of tubercles complex and irregular, each consisting of a low, smooth base, often with deeply excavated outline (Fig. 5a, d) and a smaller, domed upper portion, which is somewhat less irregular in outline and covered with small rounded bumps (Fig. 5d). Tubercles mostly separated from one another, but occasionally joined by narrow bridges (Fig. 5a). Floors of outer chorionic cell fields smooth, but partly covered with a very thin layer of irregular outline usually extending some distance from field edges, but occasionally forming narrow bridges to tubercles or completely across cell (Fig. 5d). Outer chorionic reticulum low, width 0.9–3.2 μm, consisting of a fine reticulate meshwork with a line of small (ca. 0.3–0.5 μm diameter), rather un-

Table 2. Numbers of outer chorionic tubercles in outer chorionic cells on different egg surfaces of two species of *Aedes* (n = 15).

Species	Dorsal Surface		Lateral Surface		Ventral Surface	
	Mean (±SE)	Range	Mean (±SE)	Range	Mean (±SE)	Range
Ae. vexans	8.7 ± 0.7	6–14	*		10.0 ± 0.5	7–15
Ae. infirmatus	5.5 ± 0.4	3–8	9.6 ± 0.4	7–12	3.7 ± 0.3	2–7

* Not counted.



evenly spaced (0.6–2.2 μm) round or tab-like protuberances almost always offset to one side of reticulum and often attached to adjacent cell floor (Fig. 5d). Meshwork of reticulum often overlying bases of tubercles, particularly at cell corners (Fig. 5d).

Chorion, lateral surface (ventral-dorsal transition): outer chorionic cells not polygonal, outlines much more rounded, somewhat longitudinally elongate, but also with at least one or, more frequently, two extensions in the circumferential direction (Fig. 5b). Cell length (longitudinal) 20–23 μm, width including circumferential extensions 19–30 μm, corresponding cell field dimensions 17–20 μm and 16–27 μm. Outer chorionic tubercles 7–12 in number, more than on ventral or dorsal surfaces (Table 2), large central ones often not touching outer chorionic reticulum, bridges joining adjacent tubercles quite frequent (Fig. 5b). Structure of tubercles, cell fields and outer chorionic reticulum same as on ventral surface.

Chorion, dorsal surface: shape of outer chorionic cells irregular, boundaries rounded (Fig. 5c), cells not as wide in longitudinal direction (12–19 μm) as circumferential (12–31 μm), number of tubercles 3–8, more than on ventral but fewer than on lateral surfaces (Table 2). Outer chorionic tubercles very irregular in shape, almost always touching outer chorionic reticulum on at least part of one side (Fig. 5c), detailed structure same as ventral surface except that nodular texture of top surface less clearly defined (Fig. 5e). Outer chorionic reticulum and cell fields same as on ventral surface (Fig. 5e).

Anterior pole and micropyle: outer chorionic cells become smaller towards anterior pole, numbers of outer chorionic tubercles in each cell fewer, tubercles often partly or almost completely fused (Fig. 6a). Anterior

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Fig. 4. *Ae. infirmatus.* Entire egg, lateral view; dorsal surface at left, anterior end at top. Scale = 100 μm.

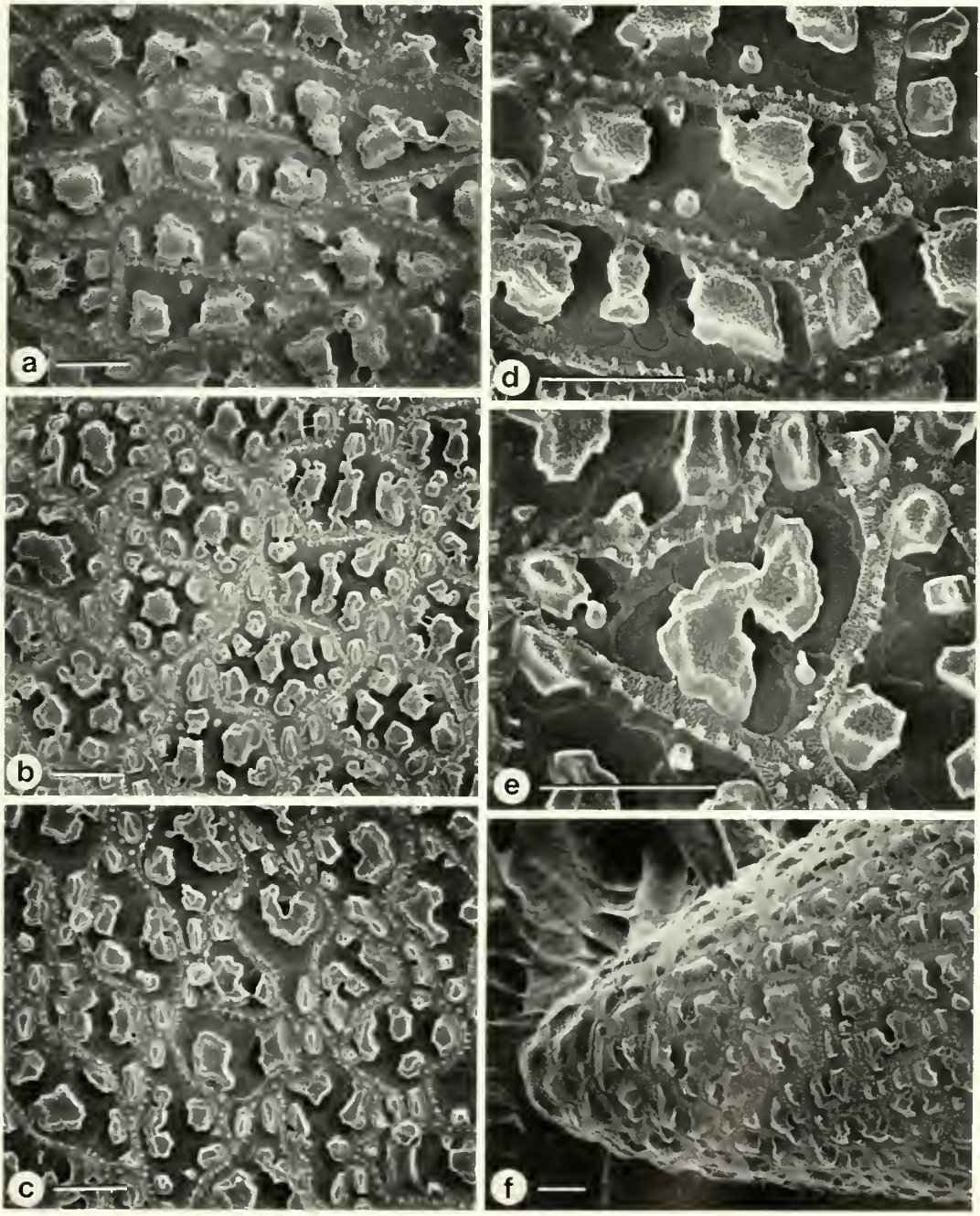

Fig. 5. *Ae. infirmatus.* (a) Outer chorionic cells, ventral surface; (b) outer chorionic cells, lateral surface; (c) outer chorionic cells, dorsal surface; (d) detail of outer chorionic cell and reticulum, ventral surface; (e) detail of outer chorionic cell and reticulum, dorsal surface; (f) posterior pole, lateral surface. Scale = 10 μm.

ring absent. Micropylar collar tapered in conformity with rest of egg and therefore not conspicuous, height 7–10 μm, variable, diameter 26–40 μm, more or less circular but not always continuous (Fig. 6b, c), internal diameter 20–26 μm, wall width 3–9 μm and very variable (Fig. 6c), interior wall appearing as a series of shallow excavations (Fig. 6b, c). Micropylar disc fairly prominent, diameter 17–19 μm, with quite conspicuous (Fig. 6c) central dome (ca. 14 μm in diameter). Micropyle roughly circular, diameter ca. 1.8 μm.

Posterior pole: outer chorionic cells diminish in size towards pole, boundaries irregular (Fig. 5f), outer chorionic cells progressively fewer in number, becoming fused to form very large tubercles, until all tubercles fused in cells crowning posterior pole (Fig. 5f).

Discussion

In the several earlier accounts of *Aedes* eggs (Horsfall and Craig 1956, Craig and Horsfall 1960, Myers 1967, Kalpage and Brust 1968, Horsfall et al. 1970), the principal characters described were color, size, shape, and the inner chorionic pattern, representing the boundaries of the chorionic cells. Keys for identifying eggs of different species could be constructed using these characters (Myers 1967, Kalpage and Brust 1968). However, examination of the inner chorionic pattern relied on phase contrast microscopy following a rather lengthy preparative procedure (Craig 1955) involving removal of the embryo and the outer chorion, then bleaching, washing, dehydrating, clearing and mounting pieces of the inner chorion in balsam. This method has the advantage that it can be carried out with minimal equipment and requires only relatively simple techniques of light microscopy. Its great disadvantage is that it destroys a major part of the intact structure of the egg. The outer chorion is complex (e.g. Figs. 2, 5) and embodies a number of characters of potential taxonomic interest.

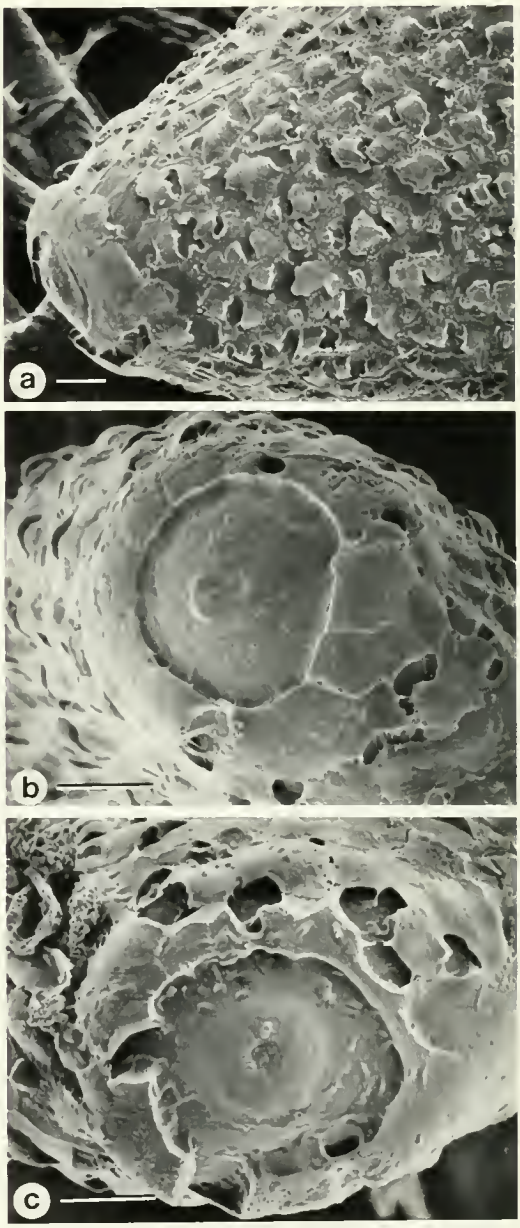

Fig. 6. *Ae. infirmatus.* (a) Anterior pole and micropylar apparatus, lateral surface; (b) top view, detail of micropylar apparatus; (c) variant of micropylar apparatus. Scale = 10 μm.

It is true that eggs handled excessively, as may be unavoidable in field collections, tend to lose at least some of the outer chorion and that outer chorionic details cannot nor-

mally be discerned by light microscopy. However, scanning electron micrographs (e.g. Figs. 1, 4) compared to phase contrast images of the chorionic obviously represent a major improvement towards understanding the intact structure and appearance of these eggs. Existing earlier descriptions are useful, but re-examination is useful in view of the enhancements obtainable from electron microscopy. The preparative work required, at least for *Aedes* eggs, is considerably less than for phase contrast microscopy of the inner chorion (Craig 1955).

In intact eggs, the main areas of new detail revealed in the electron micrograph are in the outer chorionic tubercles particularly and also the chorionic reticulum. In this paper I have not explored the several potential quantitative characters in these structures in any depth. Such an inquiry will only be useful after eggs of many other species, or different geographic populations of single species have been examined and are available on stubs for possible additional and more detailed study. Several characters might be used, such as (i) size distribution of the outer chorionic tubercles, (ii) shape of tubercles and, related to this, (iii) characteristics of their boundaries, (iv) distance separating tubercles, (v) frequency of bridges joining tubercles and, (vi) frequency of distribution in different areas of the cell field. Probably in all of these *Aedes* eggs there are at least some differences between the outer chorionic cells on different surfaces of the egg, as in *Aedes infirmatus* (Fig. 5a, b, c), and it will be necessary to select specific areas of the egg surface for study and measurement.

Acknowledgments

I thank A. Ramsey for collecting the *Ae. vexans* females and Bonnie Pattok for printing the micrographs. This paper is University of Florida, Institute of Food and Agricultural Sciences Experiment Stations Journal Series No. 9907.

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THREE NEW SPECIES OF *ACROLOPHUS* FROM THE SOUTHEASTERN UNITED STATES WITH REMARKS ON THE STATUS OF THE FAMILY ACROLOPHIDAE (LEPIDOPTERA: TINEOIDEA)

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Abstract.—Three new species of *Acrolophus*, ranging mainly through the southeastern United States are described and illustrated. ***Acrolophus heppneri*** n. sp. is the most common, widely distributed species and is reported from Grand Bahama Island west to Texas. Its larva is suspected to bore in sugarcane. ***Acrolophus spilotus*** n. sp. appears to be largely restricted to Florida. ***Acrolophus mycetophagus*** n. sp. has been reared from bracket fungus and occurs along the eastern seaboard from southern Florida to as far north as southern Virginia.

The current status of the family Acrolophidae is reviewed. The principal synapomorphies for the family are the presence of an incomplete metafurcal bridge and absence of anterior apophyses in the female ovipositor, and the partially divided spiracular plate and pronotum of the larva.

Key Words: Lepidoptera, Acrolophidae, *Acrolophus*, bracket fungus, sugarcane

Three new species of *Acrolophus* are described so that their names can be included in a proposed revision of Kimball's Lepidoptera of Florida. Together with *A. pholeter* Davis, recently described from Florida gopher tortoise burrows (Davis and Milstrey 1988), the number of *Acrolophus* reported from this state now totals 16 species, as compared to 63 from the continental United States (Davis 1983).

The systematic position of the genus *Acrolophus* has varied between recognition as either a distinct family (Dyar 1903) or as a subfamily of Tineidae (Hinton 1955). Because no discrete synapomorphy has been found to define the Tineidae, I have previously followed Hinton's treatment (based upon larval evidence) and retained the Acrolophinae within Tineidae. Recent analysis by Robinson (1989) re-establish the genus as constituting a distinct family allied to Psychidae. Robinson's conclusion was based largely on the broadly joined larval hypostomal sclerites (postgenae of Hinton, 1955) and, more significantly, the presence of a rudimentary furcal bridge (i.e. tendons) arising from the secondary arms of the metafurcasternum. Robinson interpreted this condition as a derivation of the complete bridge found in Psychidae and Arrhenophanidae, thus closely associating these two families. I concur with this interpretation and wish to add the following remarks.

Although the Tineidae currently is not a well defined family, I believe that its definition will become clearer as monophyletic groups such as the Acrolophidae are removed. The Acrolophidae are not a monogeneric family as previously supposed (Hasbrouck 1964, Robinson 1989), but one which also includes the genera *Amydria*,

Exoncotis, and *Ptilopsaltis.* The characteristics and relationships of all four genera will be treated in a future paper. In addition to the synapomorphic, incomplete metafurcal bridge, other features such as the abbreviated ovipositor, and in particular, the absence of distinct anterior apophyses, serve to characterize the group. The relative width of the hypostomal bridge is too variable (Davis 1987) within both Acrolophidae and Tineidae to be considered an autapomorphy for the former. Although all *Acrolophus* larvae I have examined (seven species) possess a broadly contiguous hypostoma (i.e. a probable autapomorphy for this genus), the hypostomal bridge of *Amydria* (Davis 1987) and *Ptilopsaltis* (Davis unpubl.) is more reduced, approximating the width occurring in such Tineidae as *Nemapogon.* The only synapomorphy I have discovered for the acrolophid larva is the partial separation of the prothoracic spiracular plate from the pronotum (Davis and Milstrey 1988). This condition most resembles the completely fused spiracular-pronotal plate in Psychidae, and thus, it may constitute another feature linking these two families.

The presence of multiple (more than five) frenular bristles in the female appears to be another character shared by the Acrolophidae, Arrhenophanidae, and Psychidae. The standard number in female Tineidae is two or three, with five bristles reported in female *Opogona sacchari* (Bojer) (Davis and Peña 1990). Female Arrhenophanidae and alate Psychidae tend to possess 6 to 12 frenular bristles, including the genus *Kearfottia,* which I regard as the most primitive psychid known. A more derived psychid genus, *Narycia,* was exceptional and found to possess only three bristles in the female.

Deposition of specimens referred to in this paper are: BMNH, for British Museum (Natural History), London, England; BrM, collection of Bryant Mather, Clinton, Mississippi; ECK, collection of Edward C. Knudson; FSCA, Florida State Collection of Arthropods, Gainesville, Florida; JBH, collection of John B. Heppner, Gainesville, Florida; MCA, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UCB, University of California, Berkeley, California; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.; and USSC, United States Sugar Corporation, Clewiston, Florida.

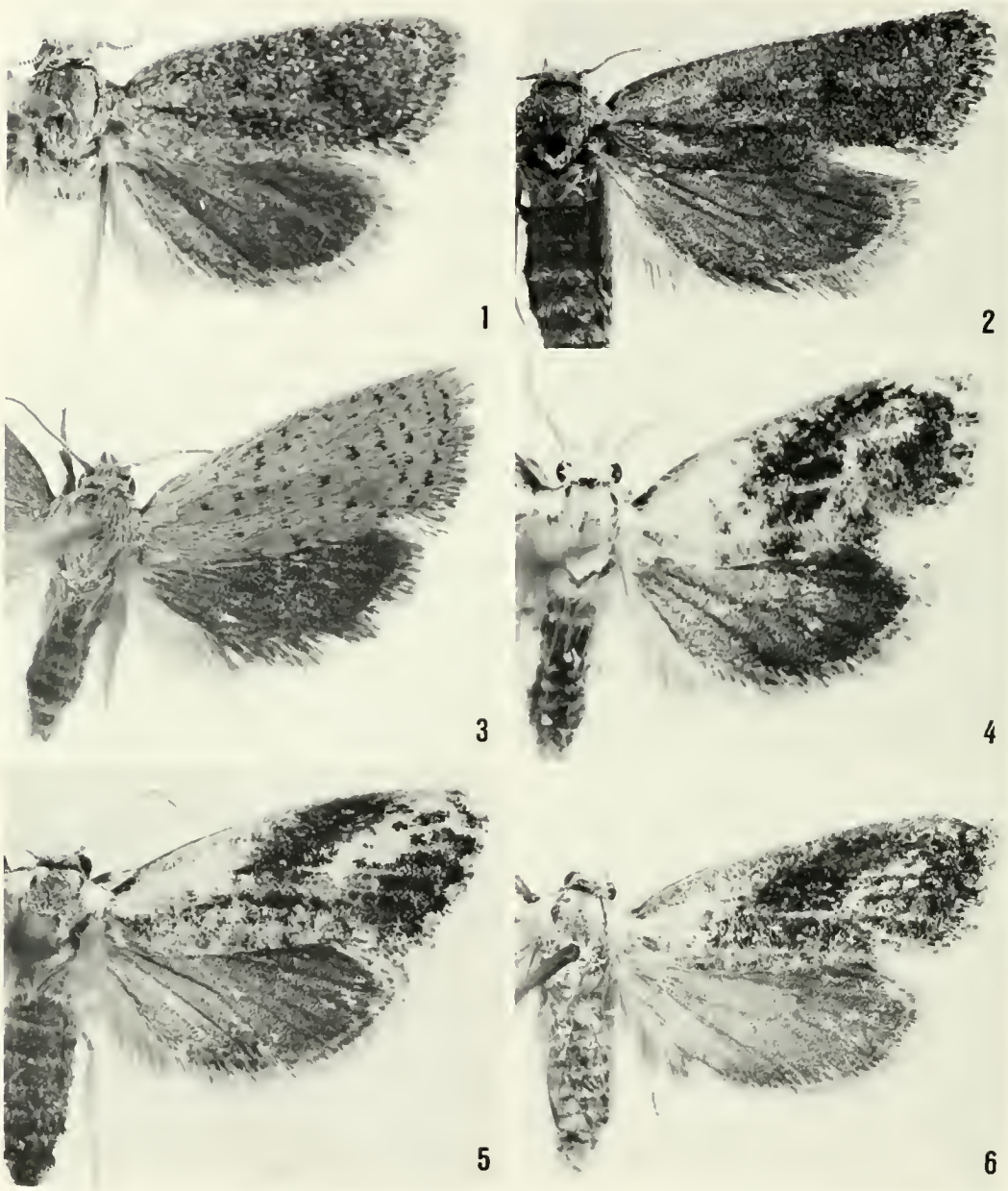
Acrolophus heppneri Davis, New Species

Figs. 1, 2, 7–12, 23

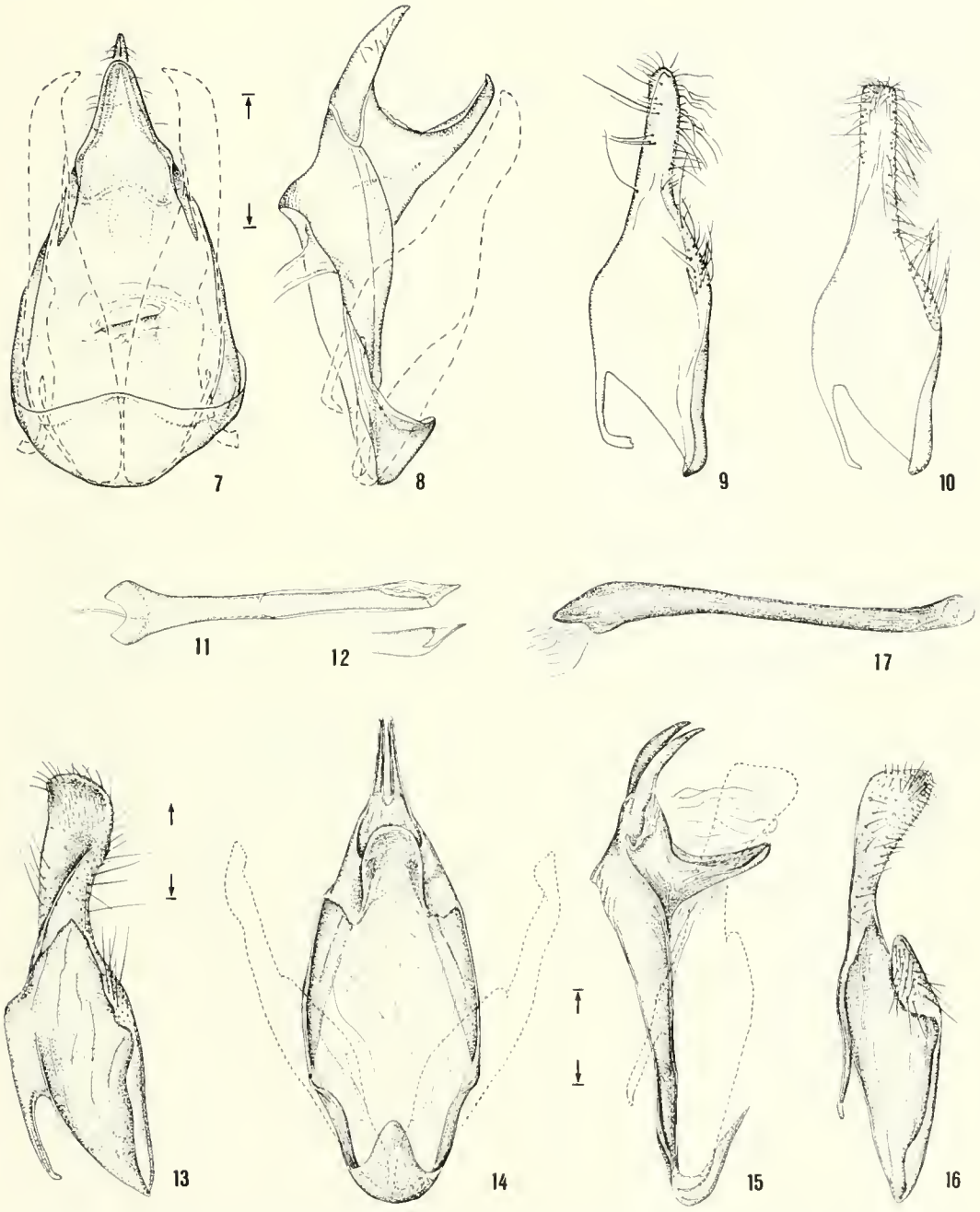
Adult (Figs. 1, 2).—*Length of forewing:* Male, 4–5.5 mm; female, 5.5–9 mm. A relatively small, uniformly brown to brownish fuscous moth with short labial palpi in male that curve upwards no further than level of antennal bases.

Head: Vestiture smooth; scales piliform, light to medium brown with paler, grayish apices. Eye small, interocular index approximately 0.63; cornea without interfacetal setae; eyelash absent. Antenna about 0.4–0.5 the length of forewing, 37–38 segmented; scape mostly light brown, without pecten; flagellomeres light brown, simple in form, and densely covered with minute sensilla chaetica. Mandible absent. Haustellum reduced, about 0.6 the length of basal segment of labial palpus. Maxillary palpus reduced to two short segments. Labial palpus 3-segmented, relatively short in both sexes, length approximately 1.75× maximum eye diameter, and upcurved in male to base of antenna; more porrect in female, predominantly light brown, tending to be paler, more whitish at base of first segment.

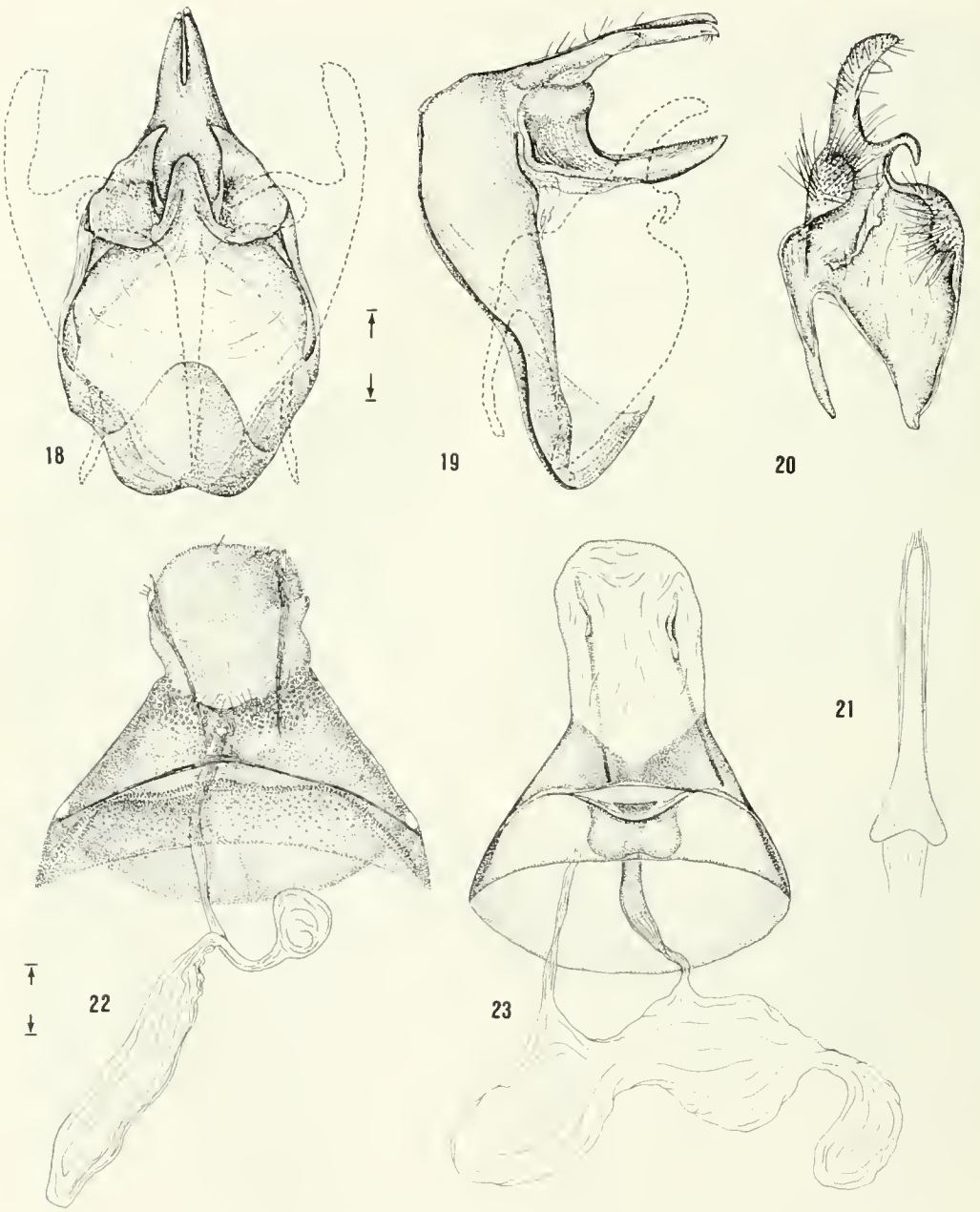
Thorax: Pronotum uniformly light to medium brown; scales of tegula usually with pale gray to white apices. Forewing uniformly medium to dark brown (darker in male), with a pair of small, barely visible, darker spots often present at base and apex of discal cell and usually more evident in lighter female; under low magnification most scales with pale bases and darker apices; R3



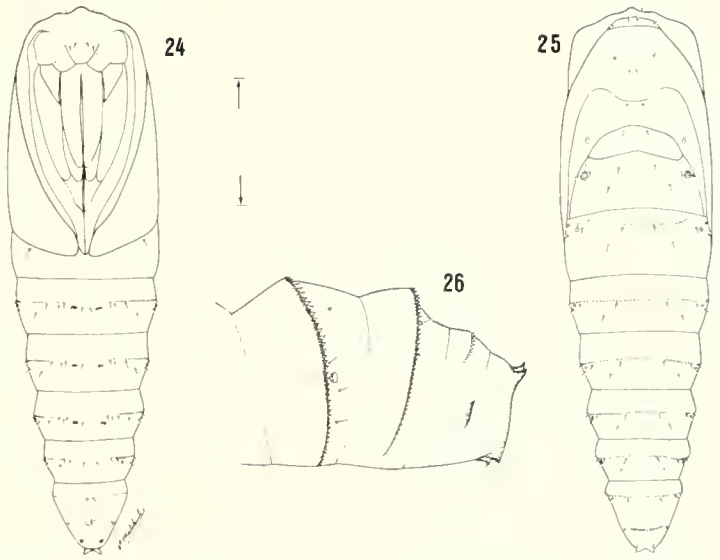
Figs. 1–6. Adult moths. 1, *Acrolophus heppneri,* holotype ♂ (5 mm). 2, *Acrolophus heppneri,* paratype ♀ (8.1 mm). 3, *Acrolophus spilotus,* holotype ♂ (6.7 mm). 4, *Acrolophus mycetophagus,* holotype ♂ (7 mm). 5, *Acrolophus mycetophagus,* paratype ♀ (11 mm). 6, *Acrolophus mycetophagus,* paratype ♀ (11 mm). (Length of forewing in parenthesis.)



Figs. 7–17. *Acrolophus,* male genitalia. 7, *Acrolophus heppneri,* ventral view. 8, Lateral view. 9, Valva, mesal-lateral view. 10, Valva, mesal-lateral view. 11, Aedoeagus, ventral view. 12, Aedoeagus, lateral view of apex. 13, *Acrolophus panamae,* valva, mesal-lateral view. 14, *Acrolophus spilotus,* ventral view. 15, Lateral view. 16, Valva, mesal-lateral view. 17, Aedoeagus, lateral view. (All scales = 0.25 mm.)



Figs. 18–23. *Acrolophus,* male and female genitalia. 18, *Acrolophus mycetophagus,* ventral view. 19, Lateral view. 20, Valva, mesal-lateral view. 21, Aedoeagus, ventral view. 22, *Acrolophus mycetophagus,* female genitalia, ventral view. 23, *Acrolophus heppneri,* female genitalia, ventral view. (All scales = 0.5 mm.)



Figs. 24–26. *Acrolophus heppneri*, pupae. 24, Ventral view (scale = 2 mm). 25, Dorsal view. 26, Lateral view of A7–10 (enlarged).

and 4 shortly stalked over one third their length; A1 and 2 faint; fringe approximately same color as forewing. Hindwing similar to forewing color, uniformly medium to dark brown, sometimes slightly darker than forewing in male. Legs generally light to medium brown dorsally; paler, more grayish white ventrally and at apices of tarsal segments; epiphysis well developed, 0.8 the length of foretibia.

Abdomen: Light to medium brown dorsally, pale buff ventrally.

Male genitalia: As shown in Figs. 7–12. Uncus triangular, apex indistinctly divided less than one sixth the length of uncus; lobes tightly appressed. Gnathos fused medially, moderately broad with rounded apex extending to apex of uncus. Juxta absent. Valva relatively simple, moderately broad at base, gradually narrowing at middle to slender, usually truncate apex (Fig. 10). Aedoeagus slender, nearly as long as valva; base broader, with median depression on anterior margin; apex with slender, flaplike extension from one side (Fig. 11); cornuti absent.

Female genitalia: As shown in Fig. 23. A single pair of moderately short, posterior apophyses present. Caudal margin of lamella antevaginalis slightly concave with a shallow, broad pocket containing a relatively broad ostium; venter of pocket (part of lamella antevaginalis) with a bilobed, sclerotized, median plate. Ductus bursae moderately large, with slightly thickened walls, constricting just before junction with corpus. Corpus bursae elongate, moderately large with three relatively distinct lobes; spicules absent.

Pupa (Figs. 24–26).—*Length* (male): 8.3 mm. Light reddish brown in color. Vertex smooth except for a pair of minute setae. Antenna to middle of A3 just short of wings which extend slightly beyond middle of A3. Frons with two pairs of minute setae. Mesonotum with two pairs of minute setae, the more anterior pair widely separated, the caudal pair arising close together near midline. Dorsum of A3–9 with a transverse ridgelike row of minute spines; spines on A4–8 nearly encircling segment at middle. A10 with a pair of short, stout cremasteral spines dorsally as well as ventrally (Fig. 26).

Holotype.—Male; Subtropical Research

Station, 4 mi [6.4 km] NW Homestead, Dade Co, Florida; 10 Jun 1974, J. B. Heppner, at blacklight, USNM slide 29852 (USNM).

Paratypes.—BAHAMAS: Grand Bahama Island: Freeport: 2 ♂, 2 ♀, 20–27 Jun 1987, W. Steiner, M. and R. Molineaux. Xanadu Beach; 2 ♂, 1 ♀, 23 Jun 1987, W. Steiner, M. and R. Molineaux. UNITED STATES: FLORIDA: Broward Co: 0.5 mi [0.8 km] S. Wiles: 1 ♂, 31 Mar 1976, D. Habeck and P. Eliazar. Dade Co: Florida City: 1 ♀, 13 May 1975, C. Covell. Homestead: 1 ♀, 11 May 1975, C. Covell; 1 ♂, 22 Nov 1972, D. Wolfenbarger. Homestead, Fuch's Hammock: 1 ♂, 16 May 1979; 1 ♂, 7 Jun 1978; 1 ♂, 8 Jun 1978; 3 ♂, 13–14 Jun 1978; 1 ♂, 11 Oct 1978; 1 ♂, 22 Oct 1978; 2 ♂, 26 Oct 1978; 4 ♂, 3 Nov 1978; 1 ♂, 14 Nov 1978; 3 ♂, 24 Nov 1978; 2 ♂, 30 Dec 1978, Dickel and Weems. Subtropical Research Station, 4 mi [6.4 km] NW Homestead: 1 ♂, 1 ♀, 24 Apr 1975; 20 ♂, 155 ♀, 9 Jun 1974; 10 ♂, 49 ♀, 10 Jun 1974, J. B. Heppner, at blacklight. Henry Co: Dunwody Plantation [19 km W of Clewiston]: 1 ♀, 17 Aug 1983, reared from larva, borer in sugarcane stalk, D. Hall. Highlands Co: Archbold Biological Station: 1 ♂, 31 Jul 1978; 7 ♂, 5 Aug 1978; 4 ♂, 8–10 Aug 1978; 6 ♂, 19 Aug 1978; 4 ♂, 27 Aug 1978; 1 ♂, 30 Dec 1978, Weems, Chance, Connors, Dickel, Frolich, and Halkin. Monroe Co: Big Pine Key, 2 km N Big Pine: 1 ♂, 27 Feb 1984, W. Steiner, A. Gerberich, and J. Lowry. TEXAS: Bexar Co: San Antonio: 2 ♀, 27 Apr 1972, B. Mather. Cameron Co: Brownsville: 1 ♀, 22 Nov 1966, A. and M. Blanchard. Padre Island: 1 ♂, 1 Mar 1978, A. and M. Blanchard. Harris Co: Bellaire: 1 ♂, 1 ♀, 20 Apr 1982; 1 ♂, 4 May 1982; 1 ♀, 10 Jul 1980; 3 ♀, 15 Sep 1980, E. Knudson. Houston: 1 ♀, 13 Mar 1969; 1 ♂, 31 May 1980; 1 ♂, 5 Jul 1980; 1 ♂, 17 Jul 1979; 2 ♂, 21 Jul 1979; 2 ♂, 23 Jul 1980; 2 ♀, 26 Jul 1979; 2 ♂, 27 Jul 1980; 1 ♀, 20 Aug 1980; 3 ♂, 13 Sep 1980; 1 ♀, 14 Sep 1965; 1 ♂, 11 Oct 1980, A. and M. Blanchard. Hidalgo Co: Bentsen State Park: 1 ♂, 11 Oct 1980, E. Knudson. Santa Ana Refuge: 1 ♂, 27 Oct 1979; 3 ♂, 30 Nov 1981, E. Knudson. Slide dissections: ECK 250, 272, 280; USNM 19954, 20369, 29848, 29850, 29851, 29960–63, 29965. Paratypes deposited in BMNH, BrM, FSCA, JBH, ECK, MCZ, UCB, USNM and USSC.

Host.—Gramineae: *Saccharum officinarum* L. (sugarcane).

Flight period.—Possibly bivoltine, with early flights from March to June and later brood July through December.

Distribution.—This species has been collected in the Bahamas (Grand Bahama Island), Florida and Texas. It is one of only a few North American *Acrolophus* that also occur in the Bahamas.

Etymology.—The specific name is proposed for John B. Heppner, who collected most of the specimens used in this study and who is currently revising Kimball's Lepidoptera of Florida.

Discussion.—*Acrolophus heppneri* exhibits a rather remarkable uniformity over its broad and somewhat disjunct range. The uniformly brown to brownish fuscous forewings normally are sufficient to distinguish it from its sister species, *A. panamae* Busck. The latter typically possesses a distinct pattern of irregular, dark fuscous bands across the forewings, more evident in the males than the females. Morphologically the two species are very close and share the peculiar, indistinctly divided apex of the uncus and similar aedoeagus. The most reliable means for distinguishing *A. heppneri* is by the more slender distal third of the valva. In addition to having a broader apex, the valvae of *A. panamae* (Fig. 13) possess a low, diagonal ridge across their inner surface that is lacking in the relatively flat valvae of *A. heppneri*.

The host association for this species is based upon a single Florida rearing record which needs to be confirmed. Label data states that the larva was boring in the stalks of sugarcane. Because of uncertainty with regard to the host record, Hall (1988) did

not include this species in his list of Florida sugarcane pests. Busck (1913) described *Acrolophus sachari* from Guyana where it was found living within silken tubes on decaying sugarcane roots underground. *Acrolophus sachari* is easily distinguished from *A. heppneri* in being larger (16–23 mm) with more heavily marked forewings. Box (1953) also lists another member of this family (*Amydria* species) as feeding on rotten, underground stems of sugarcane.

Acrolophus spilotus Davis, New Species
Figs. 3, 14–17

Adult (Fig. 3).—*Length of forewing:* Male, 5–7 mm. Female unknown. A small, brownish gray to dark fuscous moth with slightly darker, unicolorous hindwings and minutely spotted forewings. Labial palpi of male short, strongly curved dorsally to level of antennal bases.

Head: Vestiture relatively smooth; scales slender to piliform, intermixed with slightly broader scales over frons; light gray to almost white in color. Eye small, interocular index approximately 0.89; cornea without interfacetal setae; eyelash absent. Antenna about 0.4 the length of forewing, 40–43 segmented; scape uniformly light gray, without pecten; flagellomeres of similar color, simple in form and densely covered with short sensilla chaetica. Mandible absent. Haustellum minute, approximately same length as first segment of maxillary palpus. Maxillary palpus reduced to 2 short segments. Labial palpus 3 segmented, relatively short, length approximately 1.5× maximum eye diameter, mostly grayish white, slightly more gray dorsally.

Thorax: Pronotum light brownish gray to dark fuscous, same color as head and forewing. Forewing lightly speckled with darker, fuscous spots; spots small in size, most consisting of only 3–4 dark scales arranged primarily in a transverse row; R3 and 4 stalked 0.3 their length. Hindwing usually darker, uniformly fuscous (same color as dark spots in forewing). Legs mostly light gray, tending to be more white ventrally. Epiphysis well developed, approximately 0.6 the length of foretibia.

Abdomen: Light brownish gray to dark fuscous dorsally, grayish white ventrally.

Male genitalia: As shown in Figs. 14–17. Uncus elongate and divided most of its length. Gnathos fused, with relatively broad, rounded caudal margin. Juxta absent. Valva moderately slender, with gradual constriction near distal two thirds, then enlarging to form triangular apex. Aedoeagus slender, equalling length of valva, with simple apex and cornuti absent.

Holotype.—Male; Lake Placid, Archbold Biological Station, Highlands Co; Florida, 16–22 May 1964, R. W. Hodges (USNM).

Paratypes.—FLORIDA: Alachua Co: Austin Cary Memorial Forest: 1 ♂, 26 Apr 1976, Fairchild and Weems. Gainesville: 1 ♂, 7 May 1981. Escambia Co: Pensacola: 1 ♂, 16 May 1963. Highlands Co: Lake Placid Archbold Biological Station: 1 ♂, 23 Mar 1957, J. Franclemont; 1 ♂, 28 Mar 1959; 2 ♂, 30 Mar 1959; 1 ♂, 31 Mar 1959; 1 ♂, 1–7 May 1964; 1 ♂, 8–15 May 1964, R. Hodges; 4 ♂, 29 Jul 1979; 2 ♂, 6 Aug 1979; 6 ♂, 7 Aug 1979; 2 ♂, 18–19 Aug 1979; 6 ♂, 24 Aug 1979; 2 ♂, 26 Aug 1979; 1 ♂, 11–13 Sep 1979, Weems, Halkin, and Webber. Slide dissections: USNM 19810, 19811, 29846. Paratypes in FSCA, MCZ, and USNM.

Host.—Unknown.

Flight period.—Apparently bivoltine; 23 March to 15 May and 29 July to 13 September.

Distribution.—Definitely known only from Florida from Escambia County south to Highlands County. One male examined but not dissected (thus, identity questionable) from Jackson, Hinds County, Mississippi (B. Mather).

Etymology.—The specific name is derived from the Greek *spilotus* (spotted, stained) in reference to the small dark scale clusters usually present on the forewings of unrubbed specimens.

Discussion.—The speckled forewing pattern of this species normally distinguishes it from all other *Acrolophus*. The pattern may not be visible in rubbed or extremely dark specimens. The only North American species that *A. spilotus* is likely to be confused with (and only in rubbed condition) is *A. panamae* Bsk. and *A. heppneri*, new species. Male genital characters, particularly the deeply divided uncus and more slender valvae of *A. spilotus*, readily separates it from all other species including the two just mentioned. Although a large series of males have been collected at light, it is interesting to note that no females are known. Further collecting at the Archbold Biological Station in Florida, where most of the type series originated, should eventually result in females.

Acrolophus mycetophagus Davis, New Species
Figs. 4–6, 18–22

Adult (Figs. 4–6).—*Length of forewing:* Male, 5–8 mm; female, 8–11 mm. A moderately small moth with dull white forewings heavily marked with dark fuscous over distal half and uniformly dark fuscous hindwings. Labial palpi of male slightly longer than in female, curving dorsally to slightly above antennal bases.

Head: Vestiture relatively smooth; scales piliform, dull white. Eye small, interocular index approximately 0.86; cornea without interfacetal setae; eyelash absent. Antenna approximately 0.5 the length of forewing, 47–52 segmented; scape uniformly white, without pecten; flagellomeres of similar color, simple in form, and densely covered with minute sensilla chactica. Mandible absent. Haustellum reduced, about 0.8 the length of basal segment of labial palpus. Maxillary palpus reduced to 2 short segments. Labial palpus 3-segmented, relatively short in both sexes; in male upcurved to slightly beyond antennal base; shorter in female, just reaching level of antennal base, length approximately 1.5–2× maximum eye diameter; mostly white in color with basal 0.7 of first segment fuscous.

Thorax: Pronotum either uniformly white or with light brown to fuscous suffusion near center. Forewing with basal third and sometimes distal fourth dull white, occasionally with fuscous suffusion; a dark fuscous suffusion extending obliquely across wing from subapex to middle of hind margin; suffusion often more fasciate in male and more extensive in female, tending to obliterate or greatly reduce proportion of white scales over distal fourth; R3 and 4 shortly stalked; anal area slightly expanded, A 1 + 2 faint; fringe dull white to brown, often with 4–5 suffused, fuscous spots. Hindwing uniformly fuscous, fringe paler, light brown; costal margin slightly concave just basad to apex of Sc. Legs generally light brown dorsally and white ventrally with plumes of long white hairs from tibia and mesopleuron. Epiphysis well developed, about half the length of foretibia.

Abdomen: Brown to fuscous dorsally, cream colored ventrally.

Male genitalia: As shown in Figs. 18–21. Uncus elongate and divided for about half its length. Vinculum directed rather sharply ventrad. Gnathos fused medially, relatively slender, extending caudally to apex of uncus. Juxta absent. Valva highly modified, with a broad base, abruptly narrowing beyond saccular lobe to form an uncinate pollex from ventral margin, then continuing as a slender lobe to apex. Aedoeagus slender, straight, approximately two thirds the length of valva, with an acute, simple apex and cornuti absent.

Female genitalia: As shown in Fig. 22. A single pair of short, posterior apophyses present. Caudal margin of lamella antevaginalis smoothly curved. Ostium small in diameter. Ductus bursae extremely slender, moderately short, only slightly longer than posterior apophyses. Corpus bursae moderately large, with small accessory bursa; spicules absent.

Holotype.—Male; 7 mi [11.1 km] NE

Fargo, Clinch Co, Georgia; 6 May 1981, D. C. Ferguson (USNM).

Paratypes.—FLORIDA: Alachua Co: Archer Road Lab, 3 mi [4.8 km] SW Gainesville: 1 ♂, 13 Mar 1974; 1 ♂, 29 Mar 1976; 1 ♂, 2 Apr 1976; 3 ♂, 9 Apr 1975; 3 ♂, 3 Aug 1975; 1 ♂, 22 Aug 1972, J. Heppner. Edgecliff subdivision, 5 mi [8 km] S Gainesville: 1 ♂, 2 Feb 1983, em. 5 Apr 1983 from bracket fungus, D. Habeck. Gainesville: 1 ♂, 21 Apr 1968, D. Habeck; 5 ♂, 1 ♀, 2–6 May 1957, L. Hetrick; 1 ♂, 5 Aug 1957, 2 ♀, 5 Sep 1957, L. Hetrick. Charlotte Co: Punta Gorda: 1 ♂, 1 Apr 1940, H. Ramstadt. Duval Co: Jacksonville: 1 ♂, 11 Mar 1980, H. Baggett. Highlands Co: Parker Island: 1 ♂, 4–7 Jun 1964, R. Hodges. Lake Co: Leesburg: 1 ♂, 9 Sep 1963, C. Felshaw. Levy Co: Bronson: 1 ♂, 1 ♀, 5 Apr 1957, 1 ♂, 1 ♀, 25 Apr 1957, 1 ♀, 29 Apr 1957, 3 ♂, 30 Apr 1957, L. Hetrick. Liberty Co: Torreya State Park: 1 ♂, 1 May 1952, G. Walley. Manatee Co: Bradenton, Gulf Coast Exp. Station: 1 ♂, 5 Apr 1955, E. Kelsheimer. Oneco: 1 ♂, 25 Mar 1954; 1 ♂, 31 Mar 1954; 1 ♂, 2 Apr 1954, J. Franclemont; 4 ♂, Apr 1954; 1 ♂, 5 May 1954; 1 ♂, May 1954; 1 ♂, 25 Aug 1953; 2 ♂, 24 Sep 1955; 1 ♂, 27 Sep 1954, P. Dillman. Palm Beach Co: 3 mi [4.8 km] NE Pahokee: 1 ♂, 1 ♀, 31 Mar 1975, J. Heppner. Pinellas Co: St. Petersburg: 1 ♀, 17 Feb; 1 ♀, Mar; 3 ♂, 1 ♀, Apr; 2 ♂, 3 ♀, May; 1 ♀, 11 Dec; 4 ♂, 1 ♀, 15 Apr 1915, R. Ludwig; 1 ♂, 29 Apr 1914; 1 ♂, 3 Aug 1914, R. Ludwig. Sarasota Co: Siesta Key: 1 ♂, 13 Mar 1963; 1 ♂, 17 Mar 1963; 1 ♀, 25 Mar 1963; 1 ♂, 4 Apr 1970; 1 ♀, 7 Apr 1964; 1 ♂, 8 Apr 1962; 1 ♂, 10 Apr 1962; 1 ♂, 19 Apr 1962; 1 ♂, 2 May 1960; 1 ♂, 3 May 1960; 1 ♂, 5 May 1960; 1 ♂, 15 May 1960, C. Kimball. GEORGIA: Chatham Co: 1 ♂, 10 Jun 1946; 1 ♀, 30 Aug 1946, M. Mead. LOUISIANA: East Baton Rouge Par: Baton Rouge: 5 ♂, 18–26 Apr 1989, T. Friedlander. St. John Par: Edgard: 1 ♂, 9 Aug 1982; 1 ♂, 29 Aug 1982, V. Brou. NORTH CAROLINA: Columbus Co: Lake Waccamaw: 1 ♀, 25 May 1984, Steiner, Bogar, Boyd and Gerberich. Dare Co: Manteo, Roanoke Is: 1 ♂, 14 Jun 1974, S. M. Gifford. Wake Co: Raleight: 1 ♂, 16 June 1934, R. Leiby; 1 ♀, 10 Jul 1910. SOUTH CAROLINA: Berkeley Co: McClellansville, Wedge Plantation: 2 ♂, 22–23 Apr 1974, D. Ferguson; 1 ♂, 29 May 1972, 1 ♀, 3 Jun 1972, R. Dominick. VIRGINIA: Nansemond Co: Lake Drummond, Dismal Swamp: 1 ♂, 6–7 Jul 1962, D. Davis. Slide dissections: JBH 211, USNM 19812, 19813, 19815, 19816, 19831, 29847. Paratypes deposited in BMNH, FSCA, JBH, MCZ, UCB, and USNM.

Host.—Bracket fungus.

Flight period.—Possibly bivoltine, with most adults captured between Feb. 17 and June 10; a second, much smaller sample between Aug. 3 and Sept. 27. Fewer late summer records may simply represent less collecting effort.

Distribution.—This species ranges along the coastal plain of the southeastern United States from southern Florida as far north as the Dismal Swamp in southeastern Virginia.

Etymology.—The specific name is derived from the Greek *mykes* (fungus) and *phagein* (to eat).

Discussion.—*Acrolophus mycetophagus* demonstrates no affinities to any particular member of the genus. The morphology of the rather unique male genitalia supports this as well as its atypical biology. It is the first *Acrolophus* I know of to have been reared from fungus. A single specimen was reared by Dale Habeck from larva boring in an unidentified bracket fungus near Gainesville, Florida. Considering the enormous diversity of species as well as host preference (Davis 1987, Davis and Milstrey 1988) and how little we know of their biology, a fungivorus habit may eventually be discovered as not uncommon among tropical *Acrolophus*.

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SYSTEMATICS OF THE WEST INDIAN MOTH GENUS *HEURETES* GROTE AND ROBINSON (LEPIDOPTERA: LIMACODIDAE)

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Abstract.—The genus *Heuretes* Grote and Robinson, 1868, is revised. *Heuretes* was previously monotypic, comprised of *H. picticornis* Grote and Robinson, 1868, and known only from the Island of Saint Thomas, U.S. Virgin Islands. *Monoleuca albicollis* Forbes, 1930, known from Puerto Rico, is recognized as a junior synonym of *H. picticornis*. New records expand the range of *H. picticornis* to include the island of Tortola, British Virgin Islands. ***Heuretes daidaleos***, new species, and ***H. divisus***, new species, are described from the Dominican Republic. Phylogenetic analysis and transitional character states support placement of the new species in *Heuretes*. *Heuretes* appears to be closely related to other Caribbean genera *Alarodia* Moeschler and *Leucophobetron* Dyar.

Key Words: Puerto Rico, Virgin Islands, Hispaniola, Greater Antilles, systematics, cladistics, Caribbean, Zygaenoidea

In the Lepidoptera it is not uncommon for conspecific males and females to be described in different genera as different species. Epstein recognized *Monoleuca albicollis* Forbes (Limacodidae) as the junior synonym of *Heuretes picticornis* Grote and Robinson while examining a female syntype of the *H. picticornis*. Concurrently, fieldwork by Miller in the British Virgin Islands yielded good series of male specimens of a moth that matched the holotype of *Monoleuca albicollis*, known only from males. Later, Becker collected both males and females at the same locality in Puerto Rico, verifying the synonymy. These events, plus the finding of two new species from the Dominican Republic prompted us to revise and investigate the systematic placement of *Heuretes*.

This work is based primarily on specimens in the U.S. National Museum of Natural History (USNM), but we have also used material in or checked the collections of the American Museum of Natural History (AMNH), Bernice P. Bishop Museum (BPBM), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology, Zoologisches Museum der Humboldt Universitaet (ZMHB), Zoologische Sammlungen des Bayerischen Staates, and V. O. Becker private collection (VOB). Color descriptions follow Smithe (1975).

Heuretes Grote and Robinson

Heuretes Grote and Robinson, 1868: 190.—Kirby, 1892: 551.—Dyar, 1905: 382; 1935: 1130.—Van Eecke, 1925: 53.—Fletcher and Nye, 1982: 77.

Type species.—*Heuretes picticornis* Grote and Robinson, by monotypy.

Diagnosis.—Small moths, salmon to gray forewing and thorax, usually light-colored hindwing and abdomen. Conspicuous oval or quadrate spots present (at least) on male forewing apex or middle of inner margin. Male anterior thorax with dorsal collar of buff or white scales. Foreleg dark, with coxa and femur scarlet orange or dark brown. Mid- and hindlegs light colored. Hind tibia with two pairs of spurs. Male antenna bipectinate to tip or near, with light-colored scales in contrast at apex.

Discussion.—Presumed synapomorphies of *Heuretes* within Limacodidae include the scale patterns on the body and wings. These patterns include a distinct collar behind the head in males, dark-scaled forelegs in contrast to light mid- and hindlegs, and light-colored scales at the apex of the antenna in contrast to dark segments on all other segments or only near the apex.

Although found in other limacodid genera, the forewing radial vein pattern in *Heuretes*, R3+R4 branched off R2, may be independently derived. Presumed sister genera *Alarodia* Moeschler, *Leucophobetron* Dyar and *Phobetron* Huebner, possess wing venation pattern in which R3+R4 branch off R5 or nearby—the primitive condition according to Brock (1971).

Heuretes picticornis Grote and Robinson

Figs. 1, 2, 5, 6, 9

Heuretes picticornis Grote and Robinson, 1868: 190. Grote, 1882: 17; 1888: 182. Dyar, 1905: 382; 1935: 1130. Van Eecke, 1925: 53.

Monoleuca albicollis Forbes, 1930: 166. Dyar, 1935: pl. 168, fig. g [not mentioned in text]. Wolcott, 1936: 505; 1951: 746. Martorell, 1948: 549; 1976: 33, 51, 175, 252. NEW SYNONYMY, NEW COMBINATION.

Diagnosis.—Small moths with either salmon or dark-brown forewings. Front legs orange. Pale-form males have antemedian and postmedian bands on forewing visible, cream-colored hindwing; dark-form males with forewing bands not visible, either cream or dark-brown hindwing. Both male forms with conspicuous quadrate white patch medially along inner margin. Female without white patch. Male antenna broadly bipectinate, becoming unipectinate with branches abruptly shortening toward apex, scarlet-orange scales on shaft. Uncus unusually short, baglike, with lateral socii; gnathos S-shaped laterad. Valva bifid distally; aedoeagus straight basally, reaching end of valva, upturned distally.

Adult male (Fig. 1).—Forewing length 6–7 mm (one aberrant reared male, 8 mm).

Head: Frons mostly white. Vertex cream colored (54) (= color code in Smithe 1975). Antenna ca. half length of forewing; bipectinate, maximum width about 5× length of a segment, slightly tapering to near apex, then abruptly short. First two short apical segments bipectinate, remaining nine segments short, unipectinate, and bristly. Scales on shaft scarlet orange; scales on apex and pectinations buff (124). Labial palpus porrect, extending past frons, covered with scarlet-orange scales. Haustellum coiled, longer than basal segment of labial palpus.

Thorax: Dorsum with white scale bundle behind head on basal one-fifth, remainder matching forewing. Foreleg with coxa and femur scarlet orange, tibia and tarsus burnt orange (116) with dark bands distally. Midleg and hindleg a lighter cream color, with brushlike scales dorsally on tibia and tarsus. Midtibia with one pair of spurs and hindtibia with two pairs. Forewing R3 and R4 nearly fused, arising from R2 (Fig. 5). Dorsal surface of forewing in two forms, either salmon or dark brown. Diffuse postmedian and antemedian bands of dark-brown scales visible only in pale morph (Fig. 1). These bands connect, with mostly dark-brown scales from wing base to tornus, below discal cell. Conspicuous white quadrate patch on middle of inner margin, smaller dark

Figs. 1–4. 1, *Heuretes picticornis*, male wing pattern (USNM) (forewing 6 mm). 2, *Heuretes picticornis*, female wing pattern (USNM) (forewing 8 mm). 3, *Heuretes daidaleos*, male wing pattern (USNM) (forewing 6 mm). 4, *Heuretes divisus*, male wing pattern (CMNH).

spot where M2 and M3 arise from discal cell. Margins orange scarlet, preceded by dark brown scales on fringe and costal margin, scattered orange scales along veins. Ventral forewing with inner margin cream colored, base of costa scarlet, otherwise burnt orange. Dorsal hindwing cream colored, or dark brown, outer margin fringe with a few dark scales. Salmon-forewing morph with pale hindwing, dark-forewing morph with either pale or matching dark hindwing. Ventral hindwing warm buff (118) with hint of orange, more cream color along inner margin and fringe.

Abdomen: Cream colored. Genitalia as in Fig. 6. Valva bifid about three-fourth distance from base. Gnathos simple, with gently undulating margins. Uncus short, expanded ventrally above gnathos, caudal end of uncus divided. Socii forming lateral pockets with setae. Aedoeagus straight and about same length as valva; stout basally, but beyond gnathos, becoming narrow, upturned 90° distally.

Adult female (Fig. 2).—Forewing length 7.5–8.0 mm.

Head: Frons salmon colored (106). Vertex cream colored. Antenna short, ca. one-

Fig. 5. *Heuretes picticornis*, male wing venation (USNM 28034).

third length of forewing, bristly, with short pectinations, curved at tip, cream colored to near apex, dark-brown scales and lighter scales distally, nearly buff. Palpus shaped as in male, covered with warm-buff and salmon scales.

Thorax: Dorsum with brown scales, without white scale bundle of male. Legs colored as in male. Forewings as in male dark morph, less scarlet underneath, with white scale patch absent. Discal spot faint. Only pale hindwings known.

Abdomen: Genitalia as in Fig. 9. Bursa copulatrix short, with ductus seminalis broadly connected from base to middle of corpus bursae. Signum absent. Lobes of papillae anales disk shaped, irregularly toothed on margins, and covered with setae.

Types.—Lectotype female, here designated (ZMHB), and paralectotype female (AMNH) (*H. picticornis*); Holotype male, AMNH (*M. albicollis*).

Type localities.—[U.S. Virgin Islands], [Island of] Saint Thomas (*H. picticornis*); Puerto Rico, Coamo Springs (*M. albicollis*).

Hosts.—*Buchenavia capitata* (Vahl) Eichl. (Combretaceae) (USNM); *Byrsonima coriacea* (Sw.) DC (Malpighiaceae) (Martorell 1948: 549, as *B. spicata* (Cav.) Rich.; Wolcott 1951: 746, as *B. spicata*; Martorell 1976); *Cedrela odorata* Linn. (Meliaceae) (Wolcott 1951: 746, as *C. mexicana* Roem.; Martorell 1976); *Montezuma speciosissima* Sessé & Moc. (Malvaceae) (Wolcott 1951: 746; Martorell 1976); *Swietenia mahagoni* (Linn.) Jacq. (Meliaceae) (Martorell 1948: 549, 1976).

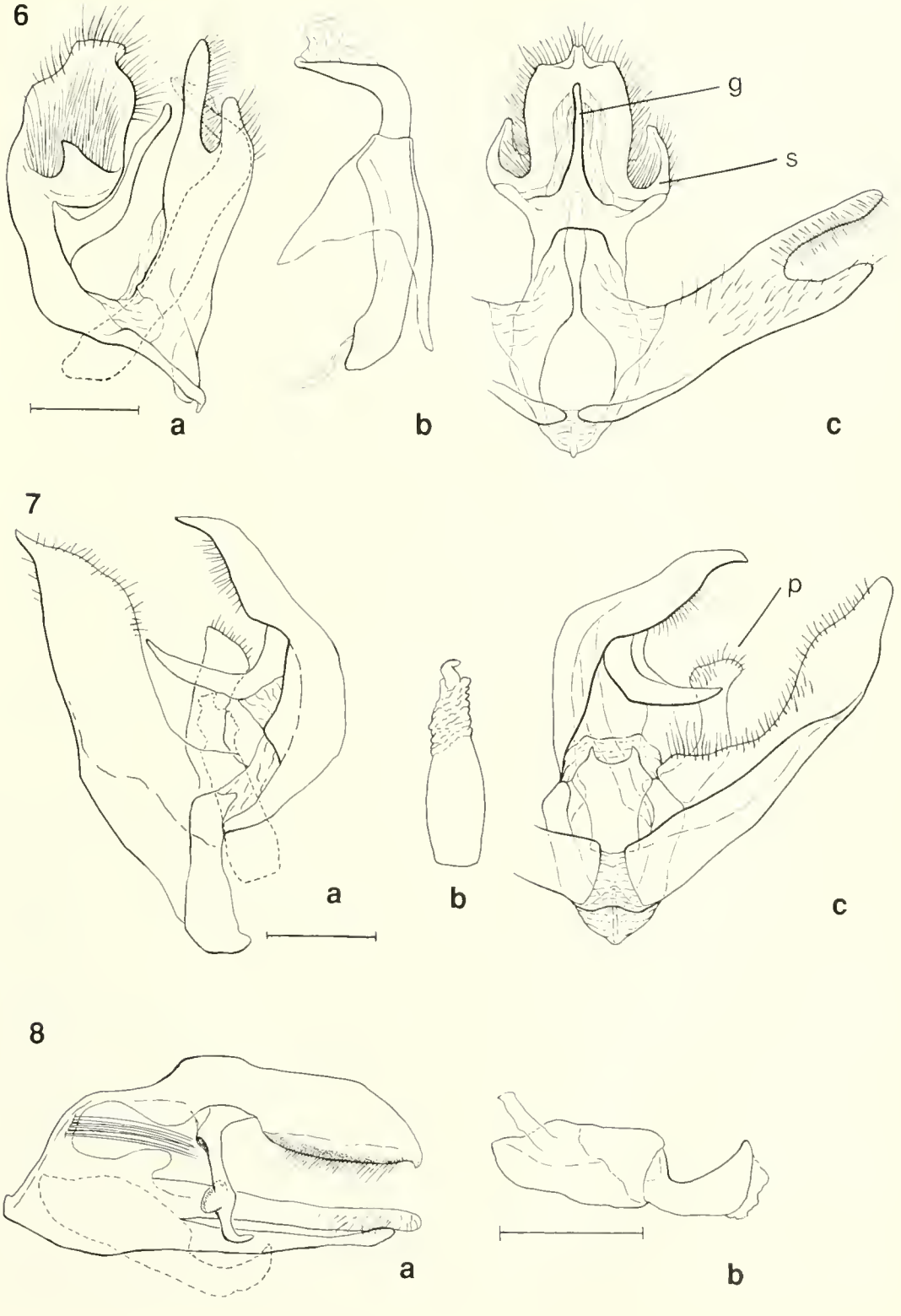
Immature stages.—This description of the previously undescribed larva is from an exuvium found inside a cocoon associated with an adult male ("Hopk. US 33101K," USNM). The exuvium was softened in 10% KOH and stored in glycerin (descriptions of tubercles are vague because precise interpretation was difficult).

Final instar: No prolegs or crochets, subdorsal row of tubercles well developed (T2–3, A2–9), extending to near middorsum, lateral tubercles short. Most subdorsal tubercles with long, filamentous hairs, maximum length ca. 1 mm, dark brown and light colored, with short lateral branches. Second or third subdorsal tubercle from anterior end with dense coat of short, filamentous hairs interspersed with long hairs, appearing darker than others. Unbranched urticating setae well developed on dorsal, basal portion of tubercles. Middorsal strip with small "skin spines."

Cocoon: Ovate, about 5 mm long, 4 mm wide, 4 mm high. Typical circular emer-

→

Figs. 6–8. 6, *Heuretes picticornis*, male genitalia: a) lateral view, right aspect (dotted outline indicates position of aedoeagus) (USNM 28109); b) aedoeagus (USNM 28025); c) ventral view of slide mounted specimen with aedoeagus removed (g = gnathos; s = socius) (USNM 28025) (scale = 0.5 mm). 7, *Heuretes daidaleos*, male genitalia: a) lateral view, left aspect (USNM 28110); b) aedoeagus (USNM 28358); c) ventral view of slide mounted specimen with aedoeagus removed, right valva (p = valval process) (USNM 28358) (scale = 0.5 mm). 8, *Heuretes divisus*, male genitalia: a) lateral view, right aspect (CMNH); b) aedoeagus (CMNH) (scale = 0.5 mm).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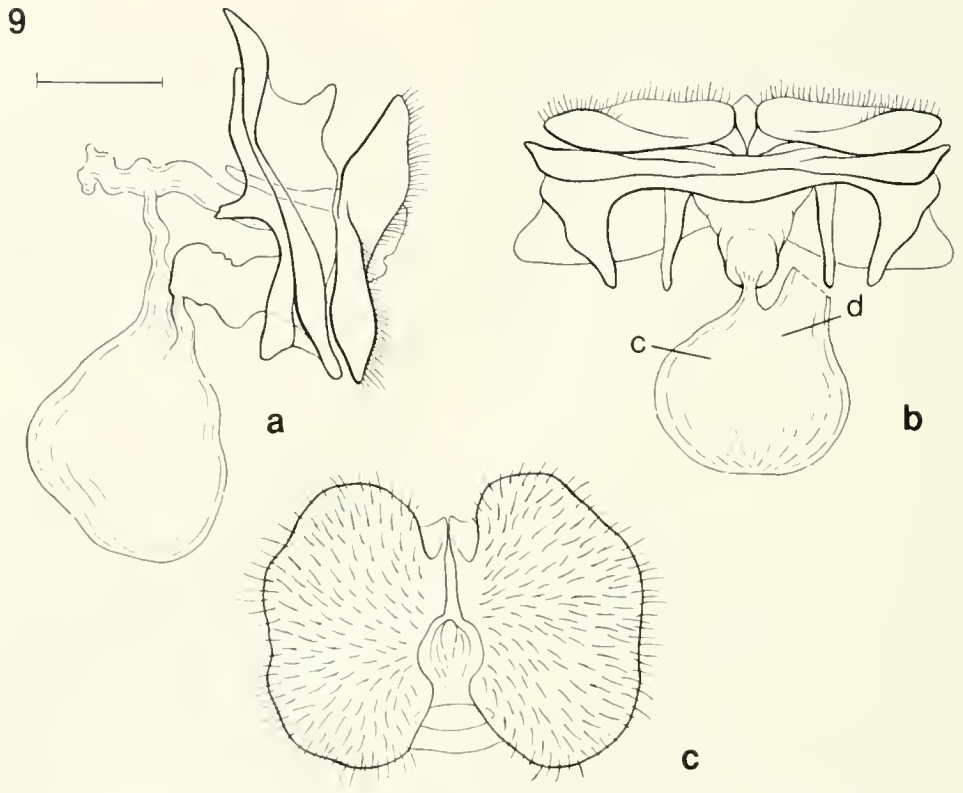

Fig. 9. *Heuretes picticornis*, female genitalia (ZMHB lectotype): a) lateral view; b) ventral view (c = corpus bursae, d = ductus seminalis; c) papillae anales (scale = 0.5 mm).

gence hatch at end. Whitish, mottled with brown, surface smooth and hard.

Flight period.—December to August.

Distribution.—Puerto Rico and the Virgin Islands, above 360 m.

Material examined.—65 males and 5 females. PUERTO RICO: Coamo Springs, 5–7 June 1915 (AMNH, holotype of *M. albicollis*); El Semil, near Villabla, 1700 feet [520 m], 10-V-1940, W. A. Hoffman (USNM); El Verde Field Station, Luqillo Experimental Forest, 435 m, 29-XII-1970 to 21-I-1971, C. P. Kimball (USNM); Hotel Barranquitas, Barranquitas, 650 m, 22–26-II-1971, Kimball (USNM); Maricao, 11–14-VIII-1987, V. O. Becker (VOB); Maricao Fish Hatchery, 23-XII-1962, P. & P. Spangler (USNM); Reserva Forestal Guajataca, 360 m, 18–28–III, 14–20-IV-1971, Kimball (USNM); Patillas, [Sierra de Cayey, ca. 20 km NE Campamento Real], 590 m, 5–25-VIII-1987, Becker (USNM, VOB); Villabla, ex *Buchenavia capitata*, Hopkins no. 33101K, I-V-1940 (USNM); U.S. VIRGIN ISLANDS: [Island of] Saint Thomas, [no further data] (ZMHB, lectotype of *H. picticornis*; AMNH, paralectotype); BRITISH VIRGIN ISLANDS: [Island of] Tortola, Mount Sage National Park, 480 m, 7–8-VII-1985, S. E. & P. M. Miller, 22–24-VII-1986, S. E. Miller & M. G. Pogue, 13–15-VII-1987, S. E. Miller & V. O. Becker, ultraviolet light trap in "aridulate rain forest" (USNM, BMNH, CMNH, LACM, VOB, BPBM).

Discussion.—The scarlet orange front coxa and femur in both male and female led to uncovering the synonymy between

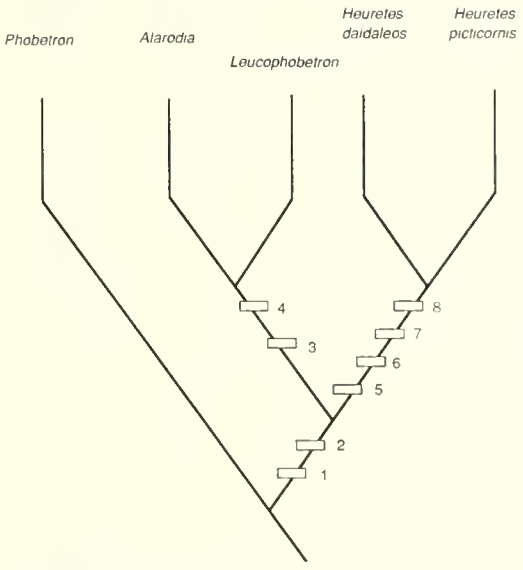

Fig. 10. Preliminary cladogram of genera related to *Heuretes* (*Leucophobetron* based on type species only). Synapomorphic characters include: 1) urticating spines in late instar larvae both branched and unbranched (known only in *A. slossoniae* and *H. picticornis*); 2) valvae asymmetrical (reversed in *H. picticornis*, see text); 3) white groundcolor; 4) uncus with dorsal process; 5) uncus with simple dorsum and curved end; 6) forewing R3+R4 branched off R2; 7) dorsal collar of white scales behind head; 8) antennal scales light colored at apex, in contrast to preceding scales.

Heuretes picticornis and *Monoleuca albicollis.* Collection of males and females at the same localities in Puerto Rico by Becker (see above) confirmed this finding, since the two types are from separate, though neighboring, islands of Saint Thomas and Puerto Rico.

This species is restricted to the Puerto Rican Bank, where it occurs between 360 and 2500 m. Martorell (1948: 549) [as *M. albicollis*] considered it "fairly common" on Puerto Rico. In the United States Virgin Islands the species has not been recorded since the original description of specimens from Saint Thomas. This could be due to lack of subsequent collecting and destruction of native forest. We record it for the first time from the British Virgin Islands, from the moist forest on the top of Tortola (termed "aridulate rain forest" by D'Arcy 1967: 392). The forest in Sage Mountain National Park on Tortola appears to be the only suitable habitat in the British Virgin Islands (see also Lazell and Jarecki 1985). The species was not found in ultraviolet light surveys on Virgin Gorda and Guana Islands.

This distribution pattern makes sense biogeographically, because the islands of the Puerto Rican Bank have been extensively connected within recent geologic time. The principal islands of the Virgin Islands (except Saint Croix) lost their connection with each other and with Puerto Rico only about 8000 to 10,000 years ago, due to eustatic rise in sea level (Heatwole et al. 1981).

Heuretes daidaleos, New Species
Figs. 3, 7

Diagnosis.—Small moth with speckled gray-brown forewing without fascia, hindwing pale buff. Small buff-colored oval spot on forewing apex. Male antenna bipectinate to apex and gently tapering; light scales throughout except dark brown subapically. Uncus oblong, tapered to well sclerotized, clawlike tip. Valvae entire, slightly asymmetrical, curvilinear process on costal base and tegumen. Aedoeagus only about half length of valvae, with short obliquely curved process at distal end. Adult female and immature stages unknown.

Adult male (Fig. 3).—Forewing length 5.5–6.0 mm.

Head: Frons buff colored (124), infuscated with gray-brown scales. Vertex cream colored (54). Antenna length as in male *H. picticornis*, but pectinations relatively short and bipectinate to tip. Pectinations at maximum ca. 3× length of a segment, gently tapering apically. Shaft and pectinations with pale-buff scales except distal fourth with dark-brown scales, buff on last two. Labial palpus and haustellum similar to *H. picticornis* except palpus buff scaled.

Thorax: Dorsum directly behind head with narrow band of burnt orange scales

(116), followed by wider collar of buff scales in basal seventh, remainder matching forewing. Foreleg as in *H. picticornis,* bands of dark scales alternating with buff rather than scarlet orange. Midleg, hindleg and thorax mostly buff ventrally. Tibial spurs as in *H. picticornis.* Forewing R veins as in *H. picticornis,* but wing shape differs. Outer angle more rounded, extending posteriorly, with inner margin short. Dorsum with dark gray-brown scales speckled over glaucus (79–80) to pale-buff scales; only one color morph known. Apex with small, conspicuous, pale-buff oval spot (0.7 mm long). Fringe dark gray brown; costal margin yellow orange. Venter with dark scales in discal cell and along outer margin; buff on inner margin and apex. Hindwing with basal and fringe scales buff, hint of gray toward outer margin.

Abdomen: Buff colored. Genitalia as in Fig. 7. Valvae entire, digitate and acuminate distally, slightly asymmetrical, left valva larger. Narrow, curvilinear process articulated with base of costa and vinculum. Uncus oblong, simple, tapering to downcurved and well-sclerotized tip. Gnathos relatively short, not reaching end of uncus. Aedoeagus short, ca. half length of valvae; globular at base, with short, curved hook pointing obliquely upward from left to right at distal end.

Type.—Holotype male, USNM.

Type locality.—Dominican Republic, Dajabon Province, Rio Massacre, Balneario Don Miguel, 7 km SW Dajabon, 40 m elevation.

Flight period.—May and July.

Distribution.—Known only from the Dominican Republic.

Material examined.—Five males from the type locality (holotype and 4 paratypes) collected 26-V-1973 by D. & M. Davis (USNM, BMNH).

Etymology.—*Daidaleos* (Gr.) means dappled or spotted, descriptive of the forewing in this species. The unlatinized nomen is treated as indeclinable in accordance with Article 31b in the International Code of Zoological Nomenclature (1985).

Discussion.—*Heuretes daidaleos* shares several male genitalic character states with *Alarodia* and *Leucophobetron* Dyar, including valval asymmetry and a costal process, absent in its congener *H. picticornis.* However, phylogenetic evidence and transitional character states in another new species below support placement of *H. daidaleos* in *Heuretes.* The costal process on the valva is believed to be plesiomorphic with respect to *Heuretes,* found in *Phobetron.*

Although the simple, oblong shape of the uncus of *H. daidaleos* appears to be closer to the limacodid groundplan than that found in *H. picticornis* or *Alarodia,* it may represent the loss of the dorsal process found in the latter group.

Heuretes divisus, New Species
Figs. 4, 8

Diagnosis.—Male genitalic characters diagnostic (see below). Known from one male specimen.

Adult male (Fig. 4).—Forewing length 5.5 mm.

Head: Frons and vertex dark brown. Antenna length as in other *Heuretes,* bipectinate to near the tip, pectinations long as in *H. picticornis,* gently tapering apically. Shaft and pectinations with dark-brown scales throughout, buff on last two. Labial palpus similar to other *Heuretes,* the former dark scaled.

Thorax: Dorsum with buff scales behind head (remainder undetermined). Foreleg with dark-brown scales. Midleg, hindleg, and ventral thorax mostly buff. Tibial spurs as in other *Heuretes.* Forewing R3 and R4 fused, arising from R2. Dorsum appears to have gray and buff scales, with salmon scales on anterior discal cell (badly rubbed).

Abdomen: Buff colored. Genitalia as in Fig. 8. Valva deeply divided less than half it s length from base into two thin digitate arms (hence the name *divisus*), the one ventrad slightly shorter. Process articulated with

base of costa and vinculum greatly reduced compared to *H. daidaleos*. Tegumen narrow with long setal brush near costa. Uncus simple, similar to *H. daidaleos* though broader. Gnathos undulated as in *H. picticornis*, but with knoblike structure ventroproximal to apex. Aedoeagus similar to *H. picticornis*, though relatively shorter and broader.

Distribution.—Known only from the Dominican Republic.

Material examined.—One male (holotype) from Pedernales Province, La Abeja, 38 km NNW Cabo Rojo, 18°09′N, 71°38′W, 1250 m, 15-VII-1987, J. E. Rawlins & R. L. Davidson (CMNH).

Discussion.—Male genitalic character states in *Heuretes divisus* are plausible transitions between character states of *H. daidaleos* and those in rather atypical *H. picticornis*. The curvilinear process at the base of its costa, much reduced compared to *H. daidaleos* and absent in *H. picticornis*, appears to be functionally replaced by the coastal arm of the deeply cleft valva. The valva in *H. picticornis*, in turn, may be derived from fusion of arms, as in *H. divisus*, to near the distal end. Other character states in *H. divisus* appear intermediate between *H. daidaleos* and *H. picticornis*, including shapes of uncus and gnathos, and relative size of aedoeagus. Shape of the aedoeagus more closely resembles that of *H. picticornis*.

Relationships of *Heuretes*

Forbes (1930) suggested that *Monoleuca albicollis* [*H. picticornis*] "might be better placed in *Protalima*," but included it in *Monoleuca* Grote and Robinson based on wing pattern. Similarity in male antennal pectinations between the type species, *Monoleuca semifascia* Walker, and *M. albicollis*, may have also influenced Forbes' generic placement. Forbes (1930) considered *M. albicollis* [*H. picticornis*] to be a "primitive" *Monoleuca* based on the "nearly united" forewing R3 and R4 (R3 and R4 are fused in North American *Monoleuca*). Other than Forbes' treatment (1930, as *Monoleuca*), the placement of *Heuretes* has remained uncertain. Grote and Robinson (1868: 190) considered *Heuretes* near *Tortricidia* Packard. Dyar (1905: 382) stated the "generic position [of *Heuretes*] is uncertain."

Heuretes is not congeneric with *Monoleuca* as the latter is presently defined, nor is *Heuretes* phylogenetically related to the *Parasa* complex of Epstein (1988) where *Monoleuca* belongs. Characters of *Monoleuca* (sensu stricto) that distinguish it from *Heuretes* are: 1) spiny type larva similar to those found in *Euclea* (Epstein 1988), 2) fused forewing R3+R4 arising from R5, rather than R2 as in *Heuretes*, 3) haustellum absent, 4) labial palpus stout, upturned, 5) signum present, and 6) one pair of hind tibial spurs.

Heuretes shares presumed apomorphic larval character states with *Alarodia* (only *A. slossoniae* known), *Phobetron*, and *Isochaetes* Dyar (Dyar 1899: 244); the "tropic hairy eucleids" of Dyar (1899). This group is defined by tubercles that are strongly developed subdorsally and weakly developed laterally, and branched, filamentous hairlike setae. Larval *Phobetron* differ from *Heuretes* and *Alarodia* by having tubercles: 1) with short and stout hairs only, 2) without unbranched urticating setae, and 3) that are deciduous, later incorporated into the cocoon. Immature characters shared between *Heuretes* and *Alarodia* include: 1) larval tubercles with long filamentous hairs, 2) short, unbranched urticating setae, and 3) white cocoons. Socii found on the uncus in *Alarodia slossoniae* (Packard) and *H. picticornis*, absent in all other taxa in both genera, are independently derived according to the phylogenetic analysis below.

Leucophobetron argentiflua (Geyer) from Cuba, the type species of *Leucophobetron*, is probably congeneric with *Alarodia* (Epstein in prep.). *Leucophobetron* includes one other species from Colombia, *Leucophobetron punctata* (Druce). Though we have not

examined it, *L. punctata* is of uncertain family status (Dyar unpublished, Nat. Agri. Libr.; Becker and Epstein in press). There are a number of taxa of this general description in several moth families in South American. Whereas, no other white species of Limacodidae are reported in the neotropics outside of the Caribbean basin.

A detailed phylogeny of the genera related to *Heuretes* and resolution of generic limits of *Alarodia* and *Leucophobetron* are beyond the scope of this paper. However, we present the results of a preliminary phylogenetic analysis that we undertook to determine the correct generic placement of *H. daidaleos* (*H. divisus* was not included because it was discovered after completion). The analysis was performed using McClade, with *Phobetron* as the outgroup. *Alarodia, Leucophobetron* (based on the type species only), and two species of *Heuretes* were the other terminal taxa. Eight characters with a total of 21 states were used in the analysis, and multistate characters were ordered with morphoclines.

Heuretes daidaleos was found to be the sister species of *H. picticornis* in two equally parsimonious cladograms (including Fig. 10, consistency index of .93). Figure 10 and a cladogram with *Alarodia* as sister group to *Leucophobetron* + *Heuretes* are supported biogeographically, since the Puerto Rican Bank (*H. picticornis*) is closer to Hispaniola (*H. daidaleos*) than it is to Cuba (*Leucophobetron* and *Alarodia*), or Jamaica (*Alarodia*).

Alarodia (Dyar 1897, 1935) and now *Heuretes* are the only genera in Limacodidae (ca. 300 neotropical species), with more than one described species in the Greater Antilles (Becker and Epstein in press). Two undescribed species, one of uncertain placement (not in *Alarodia* or *Heuretes*) from Cuba and the Bahamas (USNM, AMNH, CMNH), the other in the *Perola* complex from the Dominican Republic (CMNH), indicate that the limacodid fauna may increase with future examination. Limacodid genera *Perola* Walker and *Semyra* Walker have one described species each in the Lesser Antilles. There is one undescribed species in the *Natada* complex in this region.

Poor dispersal ability of Limacodidae (Wood 1984), and related families Dalceridae (Miller in press) and Megalopygidae, may explain their low species richness in the West Indies. Dalceridae (85 spp.) and Megalopygidae (>200 spp.), mostly neotropical families, have only one West Indian species each.

Acknowledgments

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A NEW SPECIES AND DISTRIBUTION RECORD FOR THE GENUS *CAECULUS* DUFOUR (ACARI: CAECULIDAE) FROM SOUTH DAKOTA

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Abstract.—***Caeculus lewisi,*** a new species of the genus *Caeculus,* is described and illustrated. A new distribution record for the genus *Caeculus* is recorded for South Dakota along and a key to the species of the family Caeculidae is presented.

Key Words: *Caeculus,* rake-legged mites, distribution, fungus

During the course of ecological studies in the 1970's connected with the grassland International Biome Program, invertebrate fauna of grasslands in northwestern South Dakota was investigated. At that time, a new species of *Caeculus* was discovered. The dominant vegetation of the study area was comprised of buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], blue grama [*Bouteloua gracilis* (H.B.K.) Griffiths], and western wheatgrass (*Agropyron smithii* Rydb.). Interspersed within the Pierre shale that supports these dominant grasses were outcrops of coarser-textured soil on which species more characteristic of tall-grass prairies were found. The most abundant grasses on these outcrops were big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparuis* Michx.), Indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). Field observations of this new species of mite suggested it was feeding on phlox (*Phlox* sp.) plants that were growing on the outcrops. No specimens of this new species were collected in the short-grass dominated areas surrounding the outcrops. However, observations of collected mites studied with a dissecting microscope revealed they were feeding on a fungus associated with the phlox stems. Similar studies of other plants collected from the rocky outcrop confirmed that this species of *Caeculus* feeds on fungal spores. Crossley and Merchant (1971), in laboratory observations of a species of *Caeculus,* demonstrated with radioactive tracers that their species of *Caeculus* also fed on fungus. Mites were collected in the field and transferred to petri dishes in the laboratory. Parts of plants containing fungal spores were placed in the dishes as a source of food. However, all captured individuals died without completing their life cycle. McDaniel (1979) only provided a description of the genus *Caeculus.* However, before the text was shortened for publication a key to each of the then described species of rake-legged mites from the United States and their distributions were included. That key and distribution data are presented here.

Caeculus lewisi, New Species
(Figs. 1–23)

Female (Figs. 1–6) anterior border of propodosoma projecting forward over gnathosoma with six flattened crescent shaped curved setae; two pairs of lateral eyes associated with plate region of propodoso-

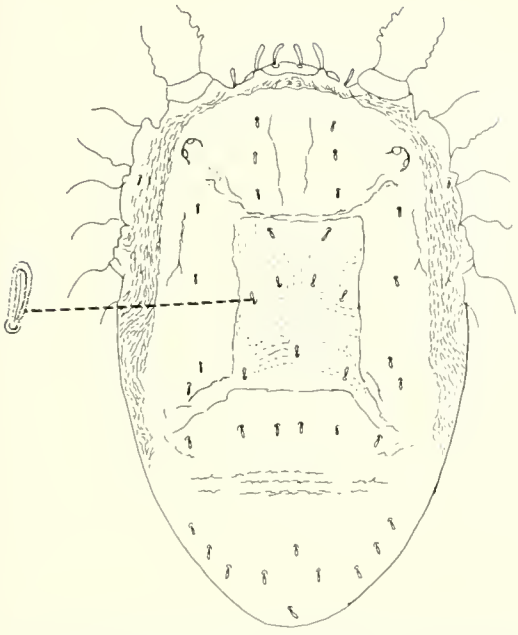


Fig. 1. *Caeculus lewisi* new species holotype female dorsal view.

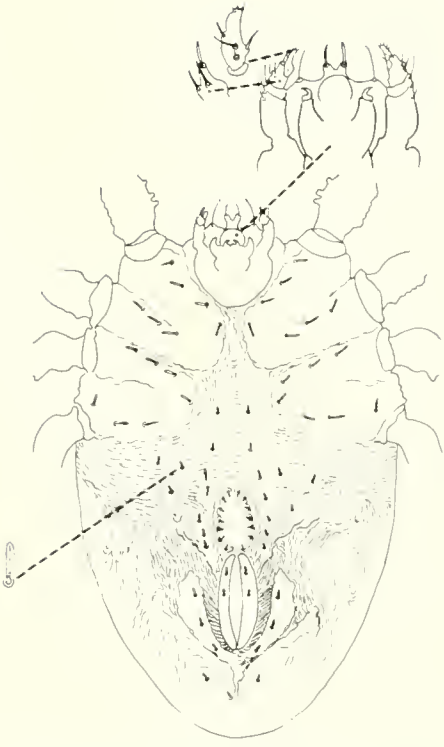
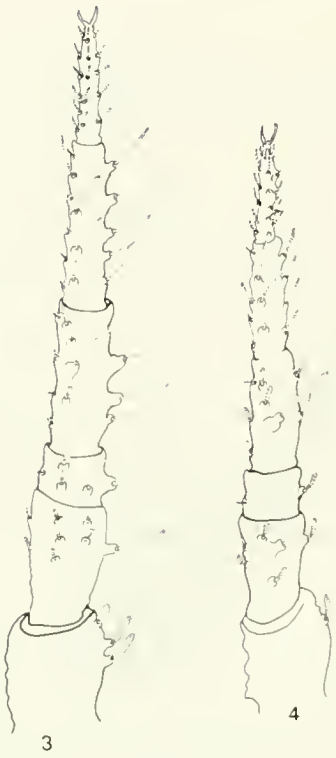


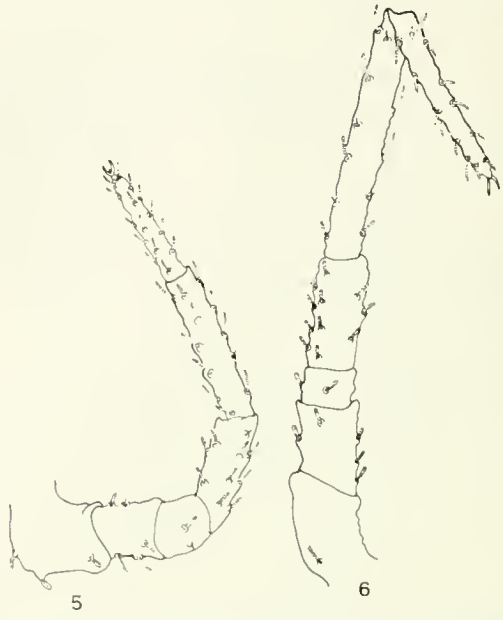
Fig. 2. *Caeculus lewisi* new species holotype female ventral view.

ma; propodosomal plate with six spatulate setae; median dorsal plate (Fig. 1) with nine spatulate setae, plate longer than wide, anterior and posterior borders subequal; lateral median dorsal plate with four spatulate setae each, three aligned in a row vertically, fourth setae paired with third lateral plate seta near posterior border of median dorsal plate; opisthosomal transverse plates fused into single transverse plate across opisthosoma, with six spatulate setae; opisthosoma with 10 spatulate setae scattered near posterior region of opisthosoma; all dorsal spatulate setae with inner plumose region; body heavily armored, wrinkled, dark brown in color; length 1.5 mm; width between eyes 0.5 mm; propodosomal region wider than opisthosomal region; ventral area below anterior projection of propodosomal plate contains a forked prominence with two spines (Fig. 2), below this structure is a crescent-shaped groove between chelicerae; palpal tibia with single terminal claw; palpal tarsus with terminal setae; first coxa with four spatulate setae; second and third coxa with three spatulate setae; fourth coxa with four spatulate setae; 20 setae in center of venter forming a double row starting from between fourth coxa, extending on either side of genital opening, each row with seven setae; three setae are grouped in a circle one either side of row of seven setae; genital opening with two rows of seven simple setae; anal opening with two pairs of simple setae surrounded by three simple setae on each side; opisthosomal region below anal opening with three setae; trochanter I with three large spatulate setae on anterior border and a single smaller setae; inner region with three spatulate setae; setal placement on rest of segments as shown in Fig. 3; setal placement on legs II, III, and IV as shown in Figs. 3–6.

Male (Figs. 7–12) anterior border of propodosoma similar to female projecting forward over gnathosoma with only four flat-



Figs. 3, 4. *Caeculus lewisi* new species holotype female, 1st and 2nd pair of legs.



Figs. 5, 6. *Caeculus lewisi* new species holotype female, 3rd and 4th pair of legs.

tened crescent-shaped, curved setae; two pairs of lateral eyes similar in structure to female; propodosomal plate with six spatulate setae; median dorsal plate (Fig. 7) with seven spatulate setae, plate longer than wide similar to female; lateral median dorsal plates with three spatulate setae each; opisthosomal transverse plate fused into single transverse plate across opisthosoma with five spatulate setae; opisthosoma with 10 spatulate setae scattered near posterior region of opisthosoma; dorsal setae similar in structure to female with inner plumose region; body heavily armored, wrinkled, dark brown in color; length 1.2 mm, width between eyes 0.5 mm; opisthosoma wider than propodosomal region; ventral area below anterior projection of propodosomal plate without forked prominence found on female; two large spine-like setae located on pronounced swellings between palps and

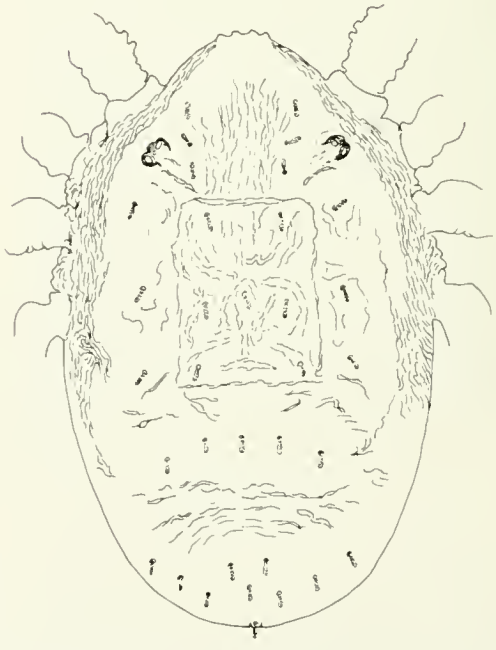


Fig. 7. *Caeculus lewisi* new species allotype male dorsal view.

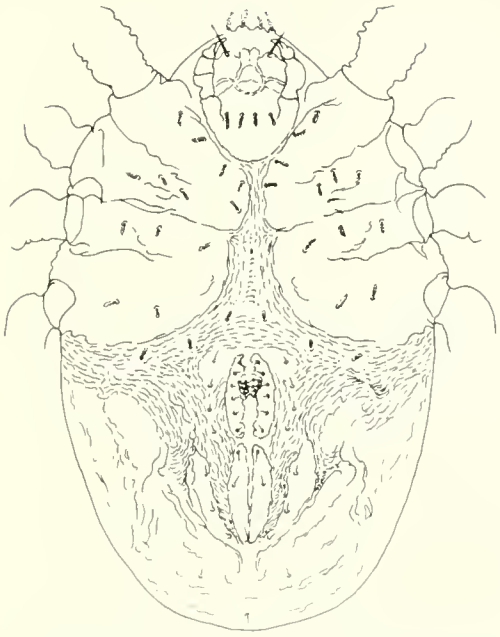
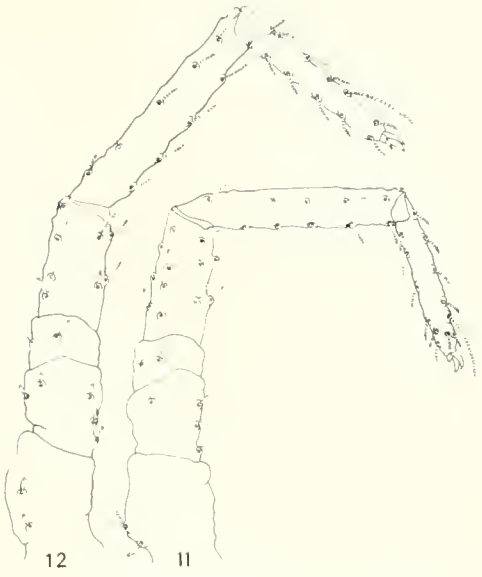


Fig. 8. *Caeculus lewisi* new species allotype male ventral view.



Figs. 11, 12. *Caeculus lewisi* new species allotype male 3rd and 4th pair of legs.

chelicerae; chelicerae reduced; four spatulate setae located below chelicera and between palps bases; first coxa with four spatulate setae; second and third coxa with three

Figs. 9, 10. *Caeculus lewisi* new species allotype male 1st and 2nd pair of legs.

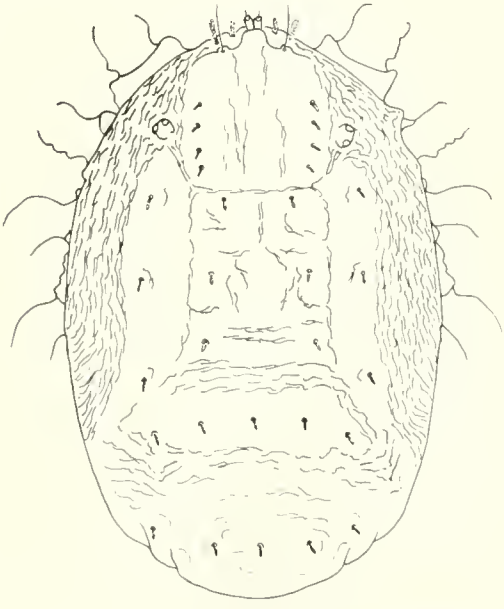


Fig. 13. *Caeculus lewisi* paratype nymph dorsal view.

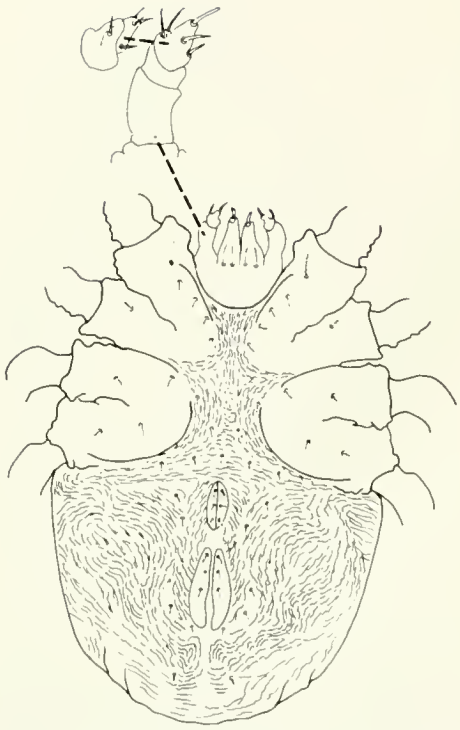
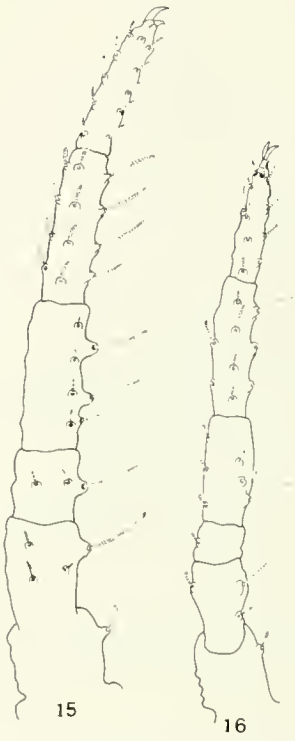


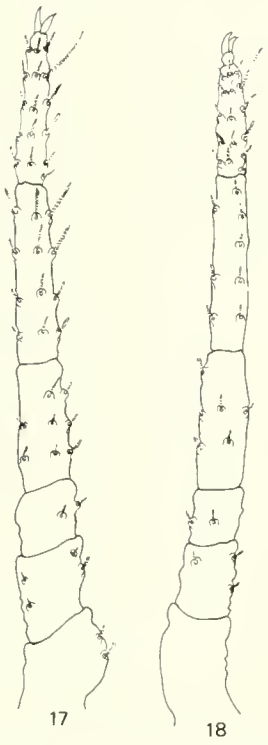
Fig. 14. *Caeculus lewisi* paratype nymph ventral view.



Figs. 15, 16. *Caeculus lewisi* paratype nymph 1st and 2nd pair of legs.

spatulate setae; fourth coxa with two spatulate setae; six setae in center of venter forming a transverse line below fourth coxa (Fig. 8); genital plates each with six simple setae; ten simple small setae associated with genital opening; anal opening with two pairs of setae surrounded by three simple setae; opisthosomal region below anal opening with three simple setae; trochanter I with three large spatulate setae on anterior border (Fig. 9); setal placement on rest of segments as shown in Fig. 9; setal placement on legs II, III, IV as shown in Figs. 10–12.

Nymph (Figs. 13–18), anterior border of propodosoma projecting forward over gnathosoma with four flattened crescent shaped setae; two pairs of lateral eyes associated with striated dorsal integument, two small setae are located on two finger-like projections of propodosomal plate; propodosomal plate with two simple, long, setae on anterior portion; propodosomal plate with eight spatulate setae, all aligned in a vertical row on lateral margin; propodosomal plate about as wide as long; lateral median dorsal plate each with three spatulate setae, all aligned in a vertical row; median dorsal plate with six spatulate setae; plate longer than wide; opisthosomal transverse plates fused into single transverse plate across opisthosoma, with five spatulate setae; opisthosoma with five spatulate setae in a transverse row in posterior region of opisthosoma; ventral palpal tibia as shown in Fig. 13; first coxa with four simple setae and a single spatulate setae; second coxa with one simple seta; third and fourth coxa with two simple setae; center of venter between fused third and fourth coxa with two pairs of simple setae; a transverse row of five simple setae located below fourth coxa; a reduced genital plate with three simple



Figs. 17, 18. *Caeculus lewisi* paratype nymph 3rd and 4th pair of legs.

setae, plate surrounded by pair of simple setae on either side (Fig. 14); anal plate with three simple setae, surrounded by three simple setae on either side (Fig. 14); opisthosomal region with a pair of setae; setal placement of legs shown in Figs. 15–18.

Larva (Figs. 19–23), anterior border of propodosoma projecting forward over gnathosoma; propodosomal plate reaching to anterior border with two spatulate setae; two pairs of lateral eyes; two spatulate setae located below lateral eyes and near posterior border of propodosomal plate; eight spatulate setae aligned in two rows of four each running from posterior border of propodosomal plate to opisthosomal region; ventral palpal tibia as shown in Fig. 20; mouthparts reduced; apex of anterior region of gnathosoma with two setae; below reduced mouth parts are four simple setae; first coxa with two setae; second coxa without setae;

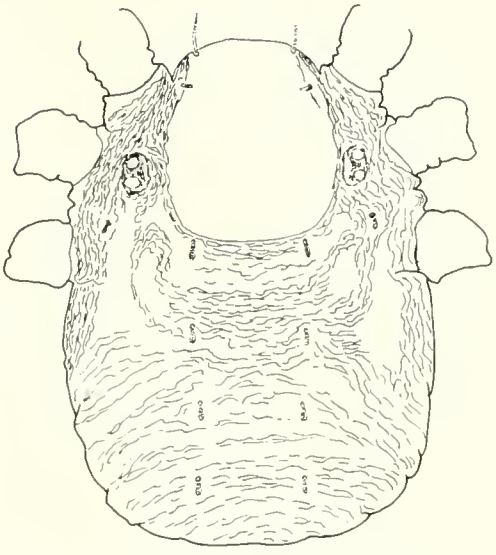


Fig. 19. *Caeculus lewisi* larva dorsal view.

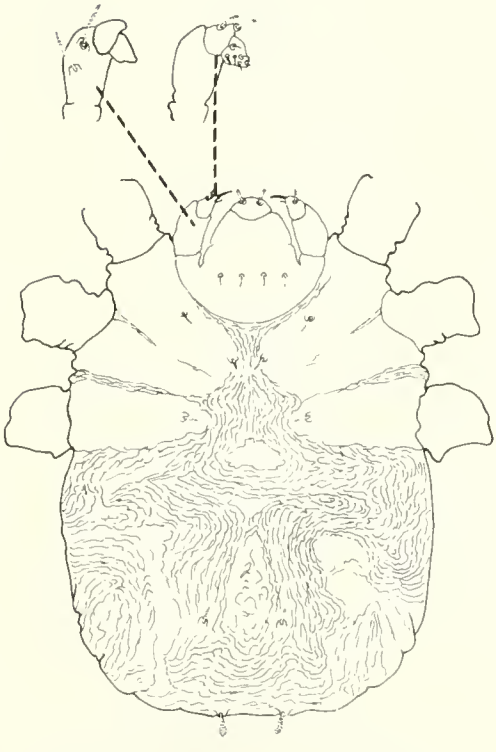
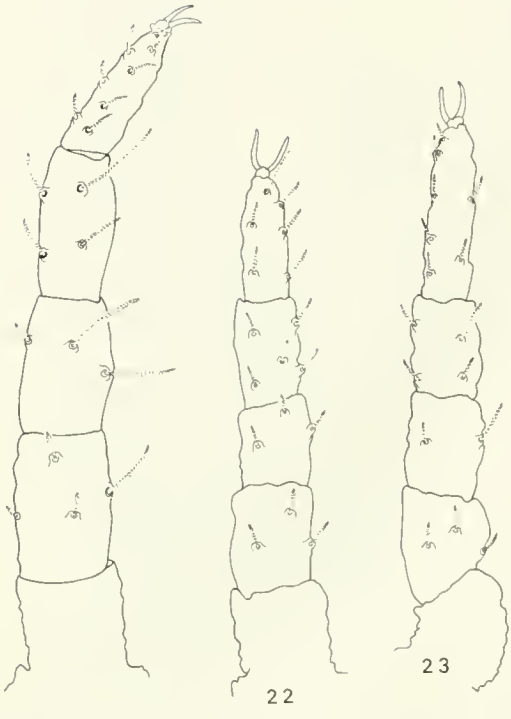


Fig. 20. *Caeculus lewisi* larva ventral view.



Figs. 21–23. *Caeculus lewisi* larval 1st, 2nd, and 3rd pair of legs.

third coxa with a single seta; venter with two pairs of setae, one pair located in posterior region of opisthosoma, other pair spatulate, located on margin of dorsal and ventral region of opisthosoma; setal placement of legs as shown in Figs. 21–23.

Female holotype collected July 16, 1972 in Butte County 10 miles north of Newell, South Dakota near Willow Creek. Allotype male, nymphs, and larvae along with 22 specimens collected at type location. The holotype and allotype along with a nymph and larva will be deposited with the USNM.

The following key constructed in 1972 from the literature was used to separate species of the genus *Caeculus*. It has been used with success to identify members of the family Caeculidae collected from Colorado, North Dakota, South Dakota, New Mexico and Texas. It is here presented for use by others that do not have access to Mulaik (1945). Mulaik's work contains no keys, but his descriptions and figures are accurate.

1. Median dorsal hysterosomal plate with 2 pairs of spatulate setae 2
– Median dorsal hysterosomal plate with more than 2 pairs of setae 3
2. Leg I with 2 setae on femur with clavate tips, 2 on tibia, and 4 on pretarsus, all located on inner margin; outer margin seta smaller than inner margin setae and curved ..... *C. clavatus* 1905 Banks (California)
– Leg I with 2 setae on femur without clavate tips, 3 on tibia, and 4 on pretarsus, all located on inner margin; outer margin seta smaller than inner setae and curved ..... *C. americanus* Banks 1899 (California)
3. Median dorsal hysterosomal plate with 3 pairs of setae 4
– Median dorsal hystersomal plate with more than 3 pairs of setae 9
4. Dorsal median hysterosomal plates I and II forming 2 pairs of small oval plates not connected at midline, each plate with 3 setae ..... *C. kerrulius* Mulaik 1945 (Texas, Utah)
– Dorsal median hysterosomal plates I and II fused into single transverse plate across opisthosomal region 5
5. First opisthosomal transverse plate with 4 setae 6
– First opisthosomal transverse plate with 5 setae 7
6. First trochanter with 3 large curved spatulate setae on anterior border; specimens normally with an incrustation of minute sand-like particles over most of body and legs ..... *C. dortheae* Mulaik 1945 (Arizona, Nevada, Texas)
– First trochanter with 2 curved setae on prominent tubercles on anterior border, one long (59 microns), club-shaped dorsomedially; without incrustation of particles ..... *C. hardyi* Mulaik and Allred 1961 (New Mexico, Texas)
7. Second opisthosomal transverse plate with 6 setae; trochanter I with 2 slightly curved cylindrical setae, posterior setae much longer than anterior setae; on anterior margin of femur is a single long seta, one on the patella, 3 on the tibia, and 4 on the pretarsus ..... *C. gretschi* Mulaik 1945 (Texas)
– Second opisthosomal transverse plate with 4 setae 8
8. Trochanter I with 2 pairs of setae, posterior seta straight, slender, as long as width of trochanter, anterior seta smaller, curved, clavate;

coxa with long slender, straight seta on anterior border, anterior to seta is a small curved clavate seta; femur and patella each with one anterior seta; tibia with 2 setae, pretarsus with 4 setae .... *C. hypopachus* Mulaik 1945 (Texas)

– Trochanter I with a single curved spatulate seta on a prominent tubercle; femur and patella with anterior setae on tubercles; tibia with 2 setae; pretarsus with 3 ..... *C. calechius* Mulaik 1945 (Montana, Texas, Utah)

9. Propodosomal plate not projecting anteriorly over the gnathosomal tubercles and not covering palps from above 10

– Propodosomal plate projects anteriorly over gnathosoma, covering gnathosomal, tubercles from above (if palps are observed it is due to mounting of specimen in a flattened position on the slide, specimens that are not on a slide will clearly show projection of propodosomal plate) 12

10. Median dorsal hystersomal plate with 13 setae arranged in a 4-4-5 sequence; left lateral metapodosomal plate with 7 setae, 2-3-2; right lateral metapososomal plate with 6 setae, 2-2-2 ..... *C. mexicanus* Mulaik and Allred 1961 (Texas)

– Median dorsal hysterosomal plate with less than 13 setae; left lateral metapodosomal plate with less than 7 setae; right lateral metapodosomal plate with less than 4 setae 11

11. Dorsal-lateral gnathosomal sensillae much expanded distally forming racket-like organs; posterior area of trochanter I set in slightly from edge ..... *C. oregonus* Mulaik and Allred 1961 (California, Oregon)
(Higgins and Mulaik 1961 placed *C. oregonus* in the genus *Procaeculus*)

– Without above characters; left and right metapososomal plate with 5 setae; distally, posterior seta of trochanter I located on posterior edge ... *C. brevis* Mulaik 1945 (Arizona, Texas)

12. Opisthosomal transverse plates I and II forming 2 pairs of small oval plates not connected at midline; on transverse plate I are II setae on each oval plate and a single seta near each inner margin of oval plate; transverse plate II with 5 setae on each oval plate ..... *C. cremnicolus* Enns 1958 (Missouri)

– Opisthosomal transverse plates I and II fused into single transverse plates across opisthosomal region 13

13. Median dorsal hysterosomal plate setae number uneven 14

– Median dorsal hysterosomal plate setae number even 15

14. Median dorsal hysterosomal plate with seven setae; dorsal plate of cephalothorax with two clavate setae near posterior corners; second transverse abdominal plate with 6 setae, each located on prominent humps on lateral margins of this plate, with one clavate seta at midline of posterior margin of dorsum ..... *C. archeri* Mulaik 1945 (Alabama, Tennessee)

– Median dorsal hysterosomal plate with 9 setae; dorsal plate of cephalothorax with 4 pairs of setae, first pair located at anterior margin, second pair near anterio-lateral margin, third and fourth pair in postero-lateral region of plate ..... *C. pettiti* Nevin 1943 (Virginia)

15. Trochanter I with 2 spatulate setae on anterior and posterior border (4 setae); 10 median dorsal hysterosomal plate setae ..... *C. tipus* Mulaik 1945 (Texas, Utah)

– Trochanter I with more than 4 spatulate setae on anterior and posterior border 16

16. Trochanter I with 3 spatulate setae on anterior and posterior borders (6 setae); 10 median dorsal hysterosomal plate setae; dorsal region of pretarsus without setae in midregion; ..... *C. valverdius* 1945 Mulaik (Arizona, Texas)

– Trochanter I with 3 spatulate setae on anterior and 2 on posterior border (5 setae); eight median dorsal hysterosomal plate setae; dorsal region of pretarsus with setae in midregion ..... *C. lewisi* n. sp. (South Dakota)

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92(4), 1990, pp. 725–731

BIONOMICS OF *EVYLAEUS COMAGENENSIS* (KNERER AND ATWOOD) (HALICTIDAE), A FACULTATIVELY POLYGYNOUS, UNIVOLTINE, BOREAL HALICTINE BEE

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Abstract.—*Evylaeus comagenensis* (Knerer and Atwood) (Hymenoptera: Halictidae) is a boreal carinate species with solitary to nearly unique semisocial or quasisocial behavior. In the Adirondacks of northern New York, it was at the southern limit of its range, which may be restricted by the deleterious effects of summer heat and drought on its brood. The brood was in exceptionally shallow subterranean clusters (combs) of delicate earthen cells. Its nest architecture, phenology, associates, and sociobiology are discussed.

Key Words: nesting, quasisocial, semisocial, polylectic

There are about 2000 species of halictine bees worldwide (Sakagami et al. 1982). They include many solitary species, as well as species that share nests in a variety of social arrangements (Michener 1974). The genus *Evylaeus* consists of small, black, inconspicuous bees that are closely related to *Lasioglossum,* and are included in this genus by some taxonomists. *Evylaeus,* a primarily Palearctic genus, includes 81 species in the Western Hemisphere (Moure and Hurd 1987). Most research concerning the biology of *Evylaeus* has been performed in Europe and Japan; only five North American species have been investigated (Moure and Hurd 1987, Packer et al. 1990a, b).

Evylaeus comagenensis (Knerer and Atwood) belongs to the 'carinate' group, in which the females have a carina on the posterior edge of the propodeum (Svensson et al. 1977), and it is closely related to *E. niger* (Viereck). Bees in this group often construct their subterranean cells so that they form delicate earthen combs, surrounded by air-filled cavities. Several *Evylaeus* species begin nesting each spring, when groups of overwintered females cooperatively construct each nest. This polygynous condition may be quasisocial if all females perform all duties, including oviposition; or it may be semisocial if there is a division of labor, with some females laying eggs and others performing other duties. In species of *Evylaeus* that may facultatively begin nests in spring polygynously, the colonies continue to produce broods in the summer in an eusocial manner. Thus the nest-founding females (foundresses) become egglayers (queens), while their daughters stay in their natal nests as workers, e.g. *E. nigripes* (Lep.) (Knerer and Plateaux-Quénu 1970) and *E. linearis* (Schenck) (Knerer 1983). *Evylaeus comagenensis* is unusual because it is univoltine, and thus does not have any eusocial phase. The only other univoltine, polygynous species is *Dialictus problematicus* (Blüthgen) from northern Japan (Sakagami et al. 1984). Strictly polygynous (quasisocial or semisocial) colonies of Hymenoptera are rare, and, therefore, *E. comagenensis* is of

unusual interest for comparative investigations of the probable evolution of insect societies.

Habitat

I discovered nests of *E. comagenensis* in 1986 during an investigation of *Andrena* (*Scrapteropsis*) *alleghaniensis* Viereck, which shared the nesting site (Batra 1990). Nests were aggregated in an insolated southeasterly facing road cut in the Adirondack Mountains of northern New York (44°12′N; 73°55′W), at an elevation of 668 m (2035′). This may be the southernmost extension of the range of this boreal bee, which occurs from north of the Arctic circle at Inuvik, N.W.T. (Sakagami and Toda 1986) to Ontario. According to Knerer and Atwood (1964), it is not found south of 45°N, but Svensson et al. (1977, Fig. 23) illustrate a record from the Appalachian Mountains in Pennsylvania. Packer (pers. comm.) found *E. comagenensis* to be rare in southern Ontario but very common to the north.

The soil in which the bees nested consisted of well-drained glacial outwash, a mixture of fine, loose, dustlike sand, pebbles, and cobbles, without surface vegetation. The surrounding area was covered with mature mixed northern hardwood and softwood forest. At the time that *E. comagenensis* was active, species of *Acer, Prunus, Amelanchier,* and *Viburnum,* as well as forest-floor herbs, were blooming. According to Knerer and Atwood (1964), this species is polylectic. I found pollen of many species in the provisions and in the digestive tracts of adults, which confirms their report.

I carefully excavated nests in May and June, 1987 and 1989. Nest contents were preserved, reared, dissected, and evaluated, and foragers were collected to determine each bee's social rank. I could not visit the site during the exceptionally hot, dry spring of 1988.

Nest Architecture, Phenology, and Associates

Each of the 21 complete nests that I examined contained a single brood-cell comb (Fig. 1). Most lacked tumuli and were closed at their entrances. Open nest entrances were irregular, cryptic, unguarded, and about 2.5 mm in diameter. The cluster of brood cells was very shallow, the topmost cells being 1.5–5.0 ($\bar{x}$ = 3.32) cm below the surface of the eroding sand. The lowest cells were 4.5–7.5 ($\bar{x}$ = 6.0) cm deep. Clusters (brood combs) were 1.5–4.0 ($\bar{x}$ = 2.6) cm high and 1.5–3.5 ($\bar{x}$ = 2.0) cm wide, and were without lateroids. They were supported in the 4–7 mm-wide cavities by several earthen pillars. Nests contained 1–12 ($\bar{x}$ = 5.5) cells. One nest that had only a single cell lacked a cavity, and a nest with two cells had an incipient cavity, indicating that the initial cells were made before the surrounding cavity was excavated. Nests that contained only one female had 1–7 ($\bar{x}$ = 3.6) cells and polygynous nests contained 6–12 ($\bar{x}$ = 9) cells. Somewhat sinuous tunnels, 4.5–7 ($\bar{x}$ = 5.5) mm in diameter, extended below the cell clusters to depths of 7.0–25.0 ($\bar{x}$ = 17.7) cm. Polygynous nests had 1–3 tunnels, but nests built by solitary females had only one tunnel.

The delicate brood cells were constructed of fine sand particles held in a stiff matrix of Dufour's gland secretion. The thinnest parts of the walls of some cells were translucent, and only 0.30 mm thick. The outline of each cell was visible on the surface of the brood comb. Cells (N = 22) were horizontal, of the usual halictine structure (Michener 1974), and 9.0–13.4 ($\bar{x}$ = 11.0) mm in length, and 4.5–5.0 ($\bar{x}$ = 4.8) mm in maximum width. The cell entrances were 1.8–3.7 ($\bar{x}$ = 2.7) mm wide, and they were filled after oviposition with a loose plug of soil that was 1.0–3.5 ($\bar{x}$ = 2.0) mm deep.

Each arched, white egg was laid on a moist, yellow, roughly oval pollen and nectar mass 4.3–4.5 mm long, 3.0–4.3 mm wide, and

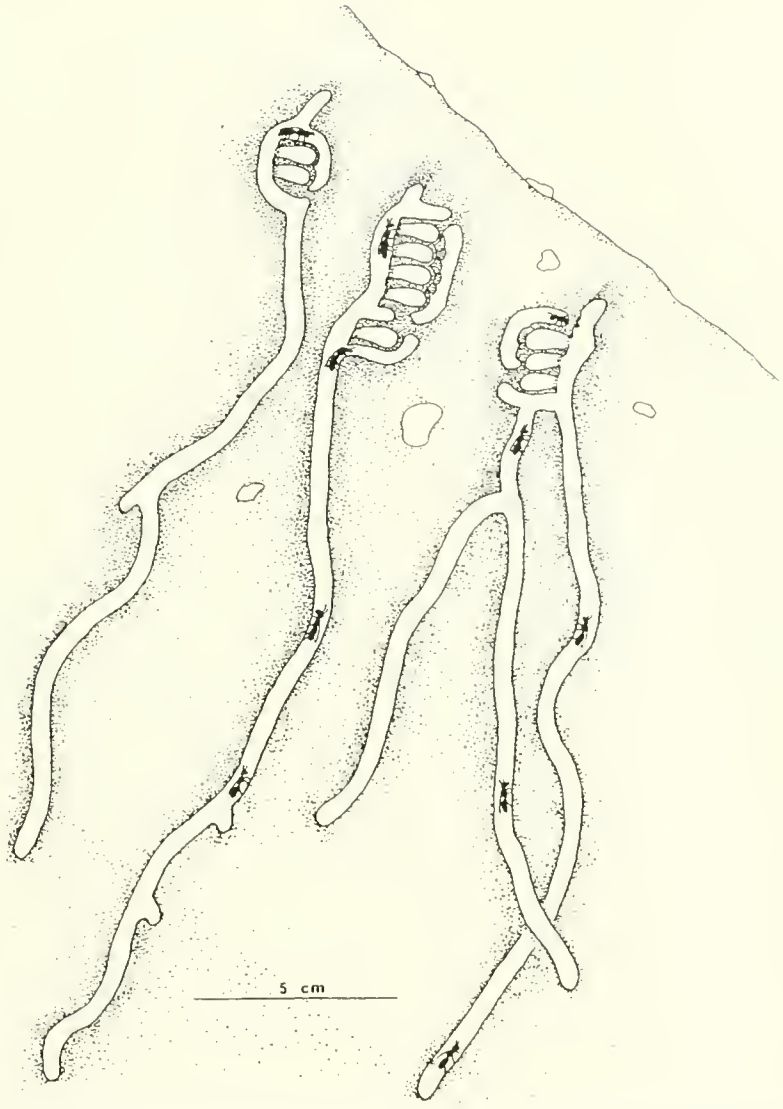

Fig. 1. Three nests of *Evylaeus comagenensis* in the sandy bank. The clusters of cells, each surrounded by an airspace, are in the sun-warmed layer near the surface. The bees will deepen the burrows below the clusters for use as hibernacula.

2.5–3.7 mm high. The provisions were longitudinally grooved on top, and were supported below on a wide pedestal as in *E. linearis* (Knerer 1983), which minimized contact with the cells.

Nests were initiated in late May. During the first week of June, eggs, larvae and pupae were present, with medium-sized to large larvae and prepupae predominating. By June 10–11 (both years) oviposition had ceased, ovaries were regressing, and the brood included larvae and pupae. I removed these and reared them in plastic tissue-culture wells at 25°C. By June 24, all were prepupae to black pupae, and from June 30 to July 2, adults emerged. Adults were kept in a small,

screened cage outdoors (in Maryland), provided with various cut flowers and sand for nesting. Males patrolled and attempted to mate at flowers, but did not inseminate females (as determined by dissection). All adults disappeared by July 15. The females burrowed into the sand and exhibited a strong photophobic response when they were removed from their burrows in August. Their burrows were initiated beneath objects on the surface of the sand, extended to the bottom of the cage, and each contained up to three females.

Hibernation in nature occurred at the ends of the burrows that extended below the cell clusters. I excavated some nests on October 30, 1987, when soil temperatures were 12°C at the surface, 10°C at 2.5 cm, 8°C at 7.5 cm, 5°C at 15 cm, and 3°C at 20 cm where bees were found. Below that level, the earth was frozen and it was not possible to excavate or locate bees. According to Sakagami et al. (1984) hibernating *Evylaeus* and other halictine bees are capable of supercooling.

The cells of *E. comagenensis* were constructed unusually near the soil surface. Such shallow placement maximized heating during the relatively few sunny days in May and early June (17%, 37%, and 24% of days in 1986, 1987 and 1989). On sunny days, the afternoon soil temperature at 2.5 cm was 10–15° warmer than soil at 15 cm, and 2–5° warmer than soil at 7.5 cm (3 measurements). When the air temperature was 32°, soil at 2.5 cm deep was 40°, and at 7.5 cm deep it was 35°. Packer (1990a, b) found that pebbles or stones just above shallow cell clusters in level soil in Nova Scotia enhance heating.

In 1989, there were fewer nests (3 nests/m^2) than in 1987 (9.6/m^2). Probably the prolonged heat (many days above 32°) and the June drought of 1988 resulted in high brood mortality. However, the population size of *Andrena alleghaniensis* at this site appeared normal (this species makes cells at 13–23 cm depth, in cooler, moister soil). *Augochlorella striata* (Prov.), another halictine that makes shallow combs, similarly suffered high pupal mortality during an unusually hot, dry summer (Packer et al. 1990b). Because *E. comagenensis* is univoltine, it has no opportunity to rapidly recover population levels. Other species of *Evylaeus* that make shallow brood cell clusters in spring make additional cells at deeper levels for summer broods, thus, they can repopulate more rapidly. Examples are *E. duplex* (Dalla Torre) (Sakagami and Hayashida 1961, 1968, Sakagami et al. 1984), *E. affine* (Smith) (Sakagami et al. 1982) and *E. nigripes* (Knerer and Plateaux-Quénu 1970). A close relative, *Evylaeus nupricola* (Sakagami), is a solitary, univoltine alpine relict species that also makes shallow cell clusters (Sakagami 1988); its distribution may similarly be limited by heat or drought.

In 1987, 82% of nests also included females and larvae of the scutacarid mite, *Imparipes apicola* (Banks) in some of the cells that contained eggs, larvae, and prepupae. In 1989, only 14% of nests included mites. According to Eickwort (1979), these mites feed on the feces of the larvae of various halictid and andrenid bees. Other associates included unidentified nematodes and fungi on feces in cells that contained healthy prepupae, and a conopid larva (probably *Thecophora occidensis* (Wlk.), Knerer and Atwood 1967) in the abdomen of a dead female. Species of *Sphecodes* (Halictidae), *Leucophora* (Anthomyiidae), and *Phrosinella aurifacies* Downes (Sarcophagidae) followed returning foragers, entered nests, or both, but none were found in cells. Larval rhipiphorids and larval Strepsiptera were on adult bees or in their crops, but none were recovered from cells or brood.

Sociobiology

One possible effect of the low population density following the 1988 drought was the lack of polygynous nests. All of the nine nests that I examined in 1989 were occupied by a single female; however, in 1987, 64%

of 12 nests were polygynous. Thus it appears that *E. comagenensis* was only facultatively polygynous. Possibly the solitary foundresses were the only survivors among sisters that would have nested together following a favorable year. Perhaps when competition for suitable nest sites became less, few females joined already occupied nests. In the strictly solitary species, *E. oenotherae* (Stevens), some females attempt to join other nesting females, but they are rejected (Knerer and MacKay 1969). Similarly, solitary *E. duplex* foundresses are aggressive toward strangers, although they later cooperate eusocially with their own daughters (Sakagami and Hayashida 1961).

All females of *E. comagenensis* were inseminated (N = 56) and male production was high in my study. Thus this bee resembled a solitary species (see Packer and Knerer 1985). In 1987 and 1989, broods were 38% and 75% male, respectively. Plateaux-Quénu (1967, Fig. 1) indicates a 50% sex ratio for this species. Fluctuating sex ratios occur also in *E. duplex* (Sakagami and Hayashida 1961).

There was neither clear division of labor nor size difference among females that shared the polygynous nests. I measured head width, ovarian and Dufour's gland enlargement, front wing nicks, and degree to which the mandibles were worn down by

Table 1. Contents of polygynous nests of *E. comagenensis* in 1987. Head width units (bee size): 1 mm = 6.4 units. The ovarian development of each female is indicated thus: A, with 2 or more eggs ready to lay; B, with large ovaries, 1 egg ready to lay; C, with moderately developed or regressing oocytes; D, with slight enlargement of oocytes; E, with no oocyte enlargement. Nicks in forewings counted (if x, wings badly damaged). Mandibular wear ranges from 1, with unworn, sharp mandibles, to 5, mandibles worn to stubs, lacking a notch.

	Adults	Number of Immatures							
			Larvae				Pupae		
Nest	Head Width (in Units), Ovary, Wing Nicks, Mandible Wear	Eggs	Small	Medium	Large	Prepupae	Male	Female	Date
1. 6 bees	13.5, C, 0, 3 13.5, B, 4, 5 13.0, C, 9, 3 13.0, B, 1, 2 12.5, D, 2, 3 12.0, B, 2, 4	1		2	3				June 1
2. 5 bees	14.0, C, 2, 4 13.5, A, 6, 5 13.0, C, 1, 2 13.0, C, 2, 5 13.0, D, 1, 2	1		3	4	3			June 4
3. 3 bees	14.0, A, 1, 5 12.0, D, 6, 3 11.0, D, 1, 5			2	2	1	1		June 4
4. 4 bees	14.0, D, 8, 3 13.0, C, X, 5 12.5, C, 2, 5 12.0, D, X, 4		1	2	5	2			June 7
5. 2 bees	14.0, D, 0, 3 13.5, E, 4, 5 (forager)		2	1	1	5	1	1	June 7
6. 3 bees	13.0, C, X, 5 12.5, E, 5, 5 12.0, E, 3, 2			2		3	3		June 10

digging, in order to detect possible castes (Table 1). Bees that had eggs ready to lay (N = 12) had mean head widths only 1.02% larger than bees (N = 9) with undeveloped ovaries (bees with partly enlarged oocytes were omitted from these comparisons). In 1987, 29% of all females had large oocytes, but in 1989, 56% of females, all of which were alone in nests, had eggs ready to lay. There was no consistent difference in wear between egg layers and non-egg layers in polygynous nests. The wings of the egg layers had 1–9 ($\bar{x}$ = 3.3) nicks, indicating probable foraging activity, and their mandibular wear was 2–5 ($\bar{x}$ = 4.0). Non-egg layers had 1–8 ($\bar{x}$ = 3.8) wing nicks and mandibular wear of 3–5 ($\bar{x}$ = 3.8).

Nests that were occupied by solitary females in 1989 had 1–7 ($\bar{x}$ = 3.6) cells; in 1987, solitary females made 2–5 ($\bar{x}$ = 3.3) cells. Polygynous nests with 3 females (1 egg layer) had 3–6 ($\bar{x}$ = 4.5) cells; a nest with 4 females (1 egg layer) had 10 cells; a nest with 5 females (1 egg layer) had 12 cells; and a nest with 6 females (4 egg layers) had 6 cells. It was difficult to estimate productivity because of the probability that most or all of the females in polygynous nests may become capable of oviposition at some time. Oophagy and drifting of females to adjacent nests may also occur. It thus appears that polygynous nests more closely approach the democratic quasisocial arrangement than the semisocial pattern of behavior, in which queens and workers are well differentiated. Packer et al. (1990a) found 1–4 females per nest in Nova Scotia, where there appeared to be some division of labor in polygynous nests.

Now that many researchers worldwide have begun to investigate the intricacies and complexities of halictine sociobiology, previously unknown and sometimes unique patterns are revealed, and previously known ones are reclassified. *Evylaeus comagenensis* has pioneered social and architectural systems that are particularly well suited to the efficient exploitation of resources during the cool, rainy, and short boreal flowering season.

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A NEW SPECIES OF *ASPHONDYLIA* (DIPTERA: CECIDOMYIIDAE) ON *BORRICHIA* (ASTERACEAE) FROM FLORIDA

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Abstract.—A new species, ***Asphondylia borrichiae***, a gall former on the apical growing region of the stems of sea daisy, *Borrichia frutescens* (L.) DC. (Asteraceae), is described with illustrations. Adults from *A. borrichiae* were reared from galls collected year-round from the salt marshes along the Gulf coast of Wakulla County, Florida.

Key Words: gall former, sea daisy

The sea daisy, *Borrichia frutescens* (L.) DC. is a fleshy salt-tolerant herb that grows in discrete patches along Florida's northern Gulf coast (Bell and Taylor 1982, Stiling et al. in prep). The apical growing region of *B. frutescens* is attacked by an undescribed species of *Asphondylia* (Diptera: Cecidomyiidae) (Gagné 1989). According to Gagné (1989), the gall is known from North Carolina, Florida, and Mexico. We are currently studying this species in both the laboratory and in the field (Stiling et al. in prep.), and describe the gall midge to provide a name for our further studies. While many species of *Asphondylia* are known, there is no modern revision with keys for identification. Further, most species have been described from adults only, a stage that is remarkably homogeneous in the genus (Gagné, pers. comm.). Most cecidomyiids are mono- or oligophagous (Gagné 1989), and because no species has been described from *B. frutescens*, we regard this gall midge from *Borrichia* as a new species. This paper describes the new species with the guidelines used in Hawkins et al. (1986). The figures should allow anyone to identify larvae and pupae of this species from *Borrichia* and compare it with other species, particularly those on Asteraceae.

MATERIALS AND METHODS

Mature galls lacking emergence holes were collected, approximately once a month, from May to August, 1989 from seven sites around the Oyster Bay area of Wakulla County, Florida. Galls were taken to the laboratory and placed in 25 dram vials with a moist piece of filter paper. The vials were checked daily and any emerged flies were immediately placed in 70% ETOH. A subsample of adults was used in the following species description. In addition, several galls were immediately dissected upon return to the laboratory and third instar larvae and pupae were extracted for illustration.

To assess gall characteristics, the maximum width of ten mature green galls with emergence holes was measured at each of the seven study sites during mid-July. On 5 September, 112 additional galls were collected from the study sites and dissected to estimate clutch size per gall by counting the number of chambers within the gall.

Asphondylia borrichiae Rossi and Strong, NEW SPECIES

Adult.—*Color:* Eyes black, scutum dark brown, abdomen light brown. *Antenna:* females, mean ratio of scape : pedicel, 2.2:1 (N = 10); mean ratio of first flagellomere :

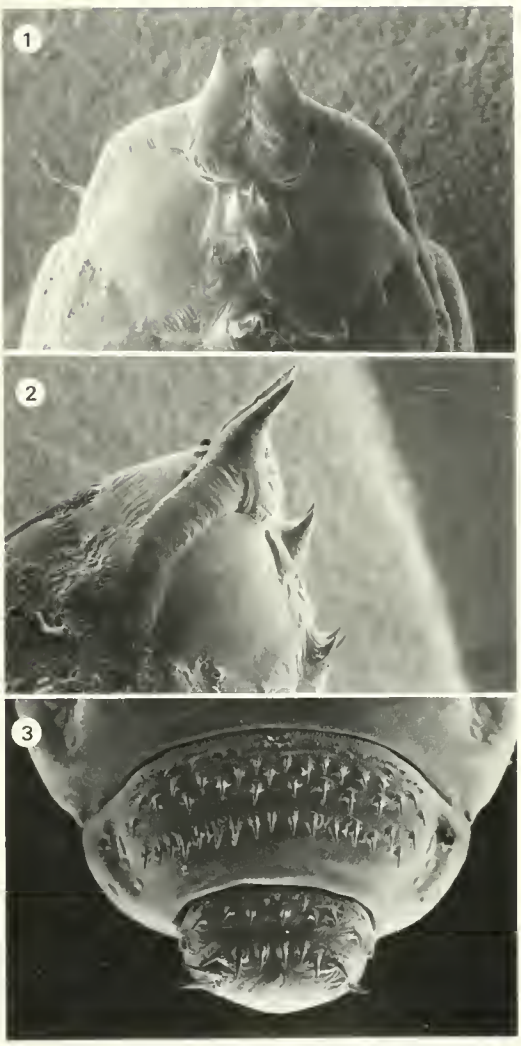
scape, 2.3:1 (N = 10); males, 2.5:1 (N = 10) and 2.2:1 (N = 10) respectively. First flagellomere cylindrical, flagellar segments successively shortened distally. Palpal segments bearing many setae, first segment tiny; second and third segments elongate, 2nd segment wider than 3rd; females, mean ratio of 1st, 2nd, and 3rd palpal segments, 1:2:5.8 (N = 10), males, 1:2:5.4 (N = 10). Wing length: males, range: 2.6–3.6 mm (N = 38), mean = 3.2 ± 0.04 (SE) mm; females, range: 2.8–3.7 mm (N = 36), mean = 3.3 ± 0.04 (SE) mm. Scutum with dorsocentral row of setae single to double approximately ⅓ from the anterior margin of scutum. Tarsal claws of similar shape among legs and between sexes and approximately as long as empodia. Mean ratio of ovipositor from base to tip of rigid shaft 2.8-times (N = 10) length of sternite 7.

Pupa (Figs. 1–3).—Antennal horns curved ventrally; serrated along interior margin. Both upper and lower frontal horns pointed anteriorly. Upper frontal horn bifid; lower frontal horn trifid. Posterior abdominal tergal spines on segments 3–8 separated from slightly smaller, anterior row of spines.

Larva (third instar) (Figs. 4, 5).—Cream to yellow in color. Spatula as in Fig. 4, quadridentate, the two inner teeth shorter than the outer pair. Four lateral papillae present on either side of the spatula. Terminal segment with one pair of dorsal papillae.

Type material.—All specimens deposited in National Museum of Natural History, Washington, D.C. Holotype.—Pupa, ex *Borrichia frutescens* gall, 5 May 1989, St. Mark's Wildlife Refuge, Wakulla County, Florida, A. M. Rossi. Paratypes: 10 females, 10 males, 5 pupae, 5 larvae, all with same data as holotype.

Galls.—These are located on the stems at the apical growing point, usually with one or more swollen pairs of leaves associated with them (Fig. 6). Galled shoots are often prevented from flowering, but flowering is occasionally seen above the galled growing point. Post-emergence galls and associated leaves rot and turn black. After the apical growing region rots, the plant sends out a new shoot from a lower meristem. Live galls were collected year-round from Oyster Bay, although gall density varied greatly throughout the year. Adults were reared every month in northwest Florida (Stiling et al. in prep).



Figs. 1–3. *Asphondylia borrichiae*. 1 and 2, Pupal head: 1, ventral; 2, lateral; 3, Pupal abdomen, dorsal. Scale: —— = 100 μm.

The maximum diameter of mature galls averaged 0.9 ± 0.02 (SE) cm (N = 70; range: 0.645–1.43). In addition, the mean number

4

5

6

Figs. 4, 5. *Asphondylia borrichiae*. 4 and 5, Larval parts: 4, spatula; 5, terminal segment, dorsal.
Fig. 6. Gall of *Asphondylia borrichiae* on its host plant, *Borrichia frutescens*; note: puparium present at 11 o'clock position.

of chambers per gall was 1.91 ± 0.08 (SE) (N = 112; range: 1–5).

Acknowledgments

We are grateful to Peter Stiling for assistance with the field work and Lawrence Abele for the use of his dissecting microscopes. We thank Sandra Silvers and Kim Riddle for their skill and patience while providing us with the electron micrographs. We especially thank Raymond J. Gagné who graciously reviewed and improved the manuscript. In addition, we thank Larry Bird for his inspiration over the past ten years. This research was supported by National Science Foundations Grant BSR-8703416 to D.R.S.

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NOTE

Examination of Some Sensory Organs on the Head of Last Instar Larvae of the Lesser Cornstalk Borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae)

The lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae) is an economic pest of several crops in the southeastern U.S., including peanut, sorghum, soybeans, and small grains (Funderburk et al. 1987. J. Entomol. Sci. 22: 159–168). Outbreak population configurations typically occur in hot, dry weather in peanuts grown in sandy soils (Mack et al. 1987. Peanut Science 14: 61–66). Larvae are usually subterranean, and may feed on pegs (gynophores), developing pods, or on plant tissue in the root-hypocotyl region.

It is probable that *E. lignosellus* larvae chemically locate their host plants and acceptable plant parts (Huang and Mack 1989. Environ. Entomol. 18(5): 763–767). It would be useful to document the sensilla in *E. lignosellus* available for host-finding, since it is the sensilla that would be involved in chemoreception. This note documents the antennal and maxillary sensilla on the head of *E. lignosellus* larvae.

Scanning electron micrographs were made

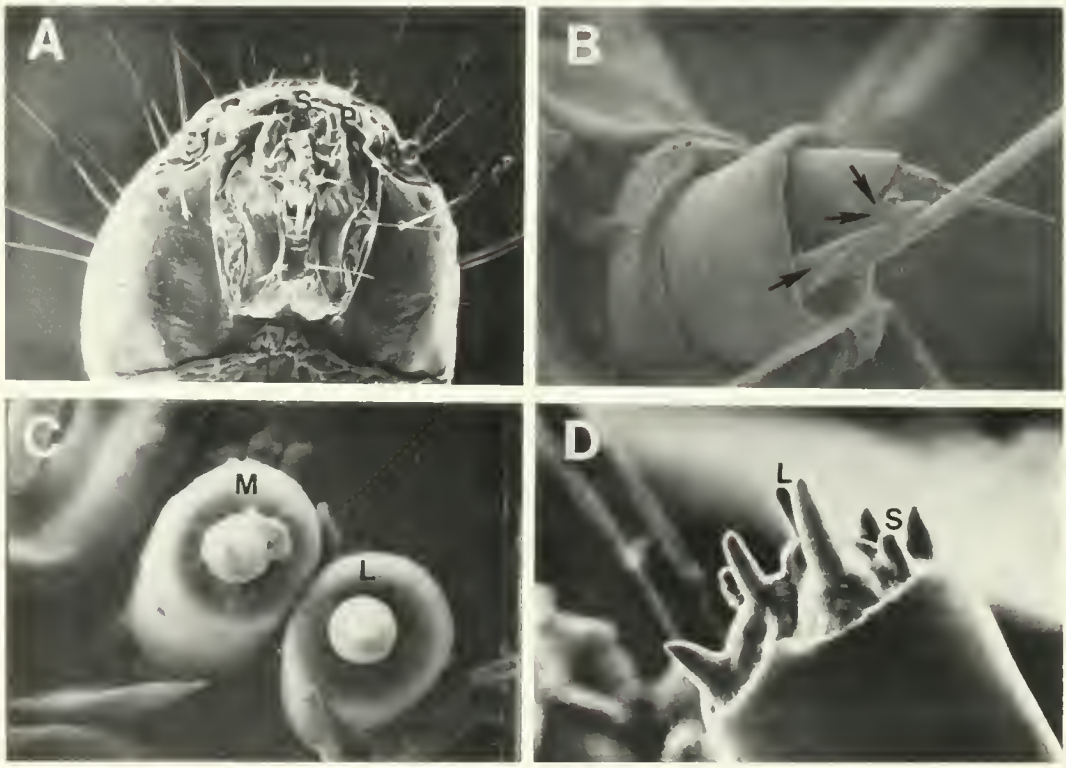

Fig. 1A–D. Scanning electron micrographs of *E. lignosellus*. A, Ventral view of the head showing the antenna (A), and sensilla styloconica on the maxillary galea (S) and maxillary palpus (P). 92×. B, Antenna with three sensilla basiconica (arrows). 850×. C, Lateral (L) and medial (M) sensilla styloconica on the maxillary galea. 4600×. D, Maxillary palpus with types (L, longer; S, shorter) of sensilla basiconica on the tip. 2900×.

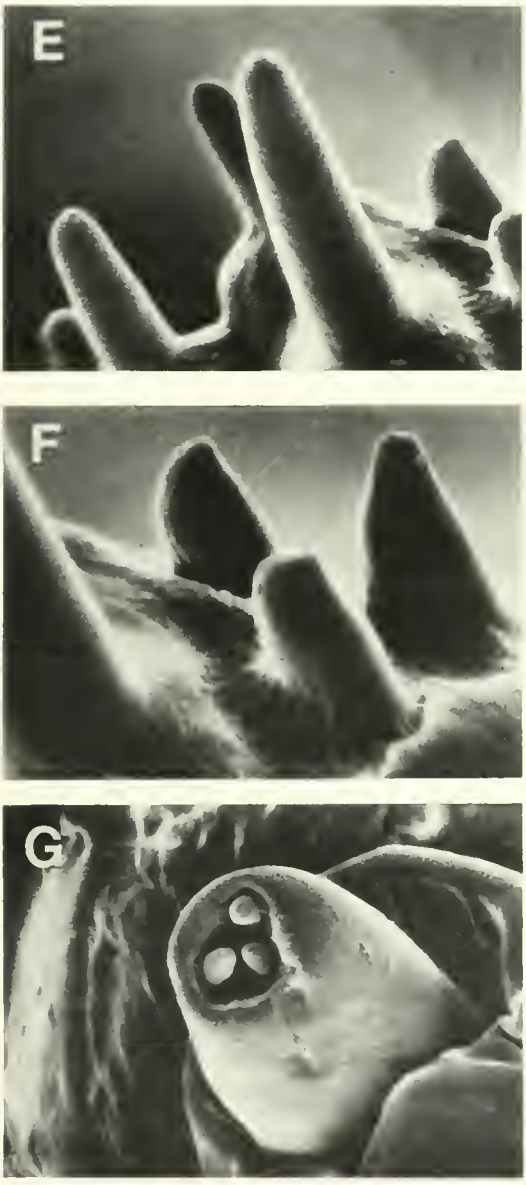

Fig. 1E–G. E, Long type of sensilla basiconica on the maxillary palpus. 8500×. F, Short type of sensilla basiconica on the maxillary palpus. 12,700×. G, A maxillary palpus with only three sensilla basiconica on its tip instead of eight. 2500×.

of the antennae, maxillary palpi, and the sensilla styloconica on the maxillae of *E. lignosellus*. Larvae were taken from a laboratory colony, immobilized with CO_2, and killed in ethanol. The heads were severed and successively dehydrated in 70%, 85%, 95%, and 100% ethanol, with 5 min in each concentration. Heads were immersed in hexamethyldisilizane for 5 min and then air-dried at room temperature. Tissue was mounted on stainless steel stubs and sputter coated with gold for microscopy.

The ventral view of the head of *E. lignosellus* (Fig. 1A) was similar to those of other lepidopterous larvae (Schoonhoven 1987. *In* Chapman et al. 1987. Perspectives in chemoreception and behavior. Springer-Verlag, NY), with each antenna possessing three sensilla basiconica (Fig. 1B). Each maxillary galea typically bore two sensillae styloconica which were nonsocket pegs with an apical papilla (Fig. 1C). Eight sensillae basiconica, with five being longer than the others, were observed on the tip of the maxillary palpi (Fig. 1D). The long sensillae basiconica had a smoother surface than the smaller ones and a small peg at their distal end (Fig. 1E), while the shorter ones were blunt with creased surfaces (Fig. 1F). It is interesting to note that not all maxillary palpi bore eight sensillae basiconica (Fig. 1G).

The antennal and maxillary sensillae of a few lepidopterous species have been examined, including the tobacco hornworm *Manduca sexta* (L.) (Hanson and Detheir 1973. J. Insect Physiol. 19: 1019–1034), the silkworm *Bombyx mori* (L.) (Morita and Yamashita 1961. J. Exp. Biol. 38: 851–861), the spruce budworm *Choristoneura fumiferana* (Clemens) (Albert 1980. Can. J. Zool. 58: 842–851), and the darksided cutworm *Euxoa messoria* (Harris) (Devitt and Smith 1982. Int. J. Insect. Morph. Embryol. 11: 255–270). All of these insects are terrestrial. The number and morphology of the sensillae on the antennae and maxillary palpi of *E. lignosellus* are very similar to those of previously described larvae. The morphology of the sensillae of *E. lignosellus*, which is primarily subterranean, do not differ from 4, primarily terrestrial larvae.

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THE TRIBE STRONGYLOGASTERINI (HYMENOPTERA, TENTHREDINIDAE) FROM TAIWAN

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Abstract.—The tribe Strongylogasterini is represented by nine species belonging to three genera in Taiwan. Two new species, ***Strongylogaster nantouensis*** and ***Pseudohemitaxonus taiwanus***, and the males of *Strongylogaster fulva* Naito and Huang and *S. formosana* (Rohwer) are described and illustrated. Three species, *Strongylogaster fulva* Naito and Huang, *Hemitaxonus nigroorolis* (Malaise) and *H. alboorolis* (Malaise) are newly recorded from Taiwan. Two genera, *Canonarea* Malaise and *Trearea* Malaise are new synonyms of the genus *Hemitaxonus*. The genus *Pseudohemitaxonus* is a new record in Taiwan. A key is given to separate the genera and species of the tribe from Taiwan.

Key Words: *Strongylogaster, Hemitaxonus, Pseudohemitaxonus*

Naito (1975) discussed the monophylety of five related genera, *Eriocampidea, Hemitaxonus, Pseudohemitaxonus, Nipponorhynchus* and *Adelesta*, in the subfamily Selandriinae. The Strongylogasterini, one of five tribes of the subfamily, consists of these five genera and their two related genera, *Strongylogaster* and *Canonias*. The morphological characters may be highly variable in this tribe (Smith 1969), but the members share the following characters: rather long and slender sawflies exclusively associated with ferns; antenna 9-segmented with flagellar segments gradually reduced in length towards apex; fore wing with vein Rs+M curved towards stigma and anal cell usually with suberect crossvein, if absent, prepectus represented by raised shoulder; hind wing with two closed middle cells; and tarsal claw slender, slightly bent at apex.

In Taiwan, this tribe was known by four species belonging to two genera (Takeuchi 1941): *Strongylogaster lineata* (Christ), *S. formosana* (Rohwer), *S. abdominalis* (Takeuchi) and *Hemitaxonus formosanus* Takeuchi. The present study, based on specimens collected by some Japanese entomologists and specimens deposited in the Taiwan Agricultural Research Institute, revealed the occurrence of nine species in three genera, *Strongylogaster, Hemitaxonus*, and *Pseudohemitaxonus*. Of these, one species of *Strongylogaster* and one species of *Pseudohemitaxonus* are new to science, and another species of *Strongylogaster* and two species of *Hemitaxonus* are newly recorded from Taiwan. Two genera, *Canonarea* and *Trearea* described by Malaise (1947) based on species from Burma, are here regarded as synonyms of *Hemitaxonus*.

KEY TO GENERA AND SPECIES OF THE STRONGYLOGASTERINI KNOWN FROM TAIWAN

1. Posttergite about as wide as scutellum. Anal cell of hind wing sessile or with short petiole at most as long as greatest breadth of cell. Propodeum normal, not excised at center 2
– Posttergite about 1.5 times as wide as scutellum. Anal cell of hind wing with long petiole about 1.5× greatest breadth of cell. Propo-

deum deeply and broadly excised at center . . . . . (*Pseudohemitaxonus* Conde) *P. taiwanus* n. sp.

2. Prepectus represented by raised shoulder, separated from mesepisternum by furrow. Anal cell of fore wing without crossvein (if present, sawsheath bifid at apex in dorsal view) . . . . . (*Strongylogaster* Dahlbom) 3
– Prepectus flat, represented by distinct sclerite, separated from mesepisternum by suture. Anal cell of fore wing with suberect crossvein . . . . . (*Hemitaxonus* Ashmead) 7
3. Head with large separate punctures. Frontal area in form of raised platform, not surrounded by distinct raised carina. Tarsal claw with large inner tooth about ½× outer one. Sawsheath with large leaflike scopa 4
– Head without large punctures. Frontal area surrounded by sharp raised carina. Tarsal claw simple or with very small inner tooth. Sawsheath with small apical projection or simple, not divided at apex in dorsal view (Fig. 4) . . . 5
4. Propodeum reticulate and dull. Clypeus narrowly emarginate in front to depth of about ⅓ its medial length. Head and thorax black in female. Second tergite rufous (sometimes with black mark) in male . . . . . *Strongylogaster lineata* Christ
– Propodeum smooth and polished. Clypeus broadly emarginate in front to depth of about ¼ its medial length. Head and thorax brownish in female. Second tergite black with apical margin rufous in male . . . . . *Strongylogaster fulva* Naito and Huang
5. Anal cell of hind wing with petiole. Tarsal claw simple, without inner tooth. Sawsheath divided at apex, with small apical projection. Hind femur entirely yellowish 6
– Anal cell of hind wing sessile. Tarsal claw with small inner tooth. Sawsheath simple, not divided at apex in dorsal view (Fig. 4). Basal half of hind femur black . . . . . *Strongylogaster nantouensis* n. sp.
6. Clypeus white. Abdomen black to dark brown . . . . . *Strongylogaster formosana* (Rohwer)
– Clypeus black to dark brown. Abdomen with 2nd to 6th terga rufous . . . . . *Strongylogaster abdominalis* (Takeuchi)
7. Anepimeron without membranous area. Anal cell of hind wing sessile. Tarsal claw with small inner tooth. Abdomen black with 3rd to 5th or 6th terga rufous 8
– Anepimeron with large membranous area. Anal cell of hind wing with petiole. Tarsal claw simple, without inner tooth. Abdominal terga usually entirely rufous . . . . . *Hemitaxonus formosanus* Takeuchi
8. Clypeus white. Hind femur yellow. Malar space about as long as diameter of front ocellus . . . . . *Hemitaxonus albooralis* (Malaise)
– Clypeus black. Hind femur blackish with apical half yellow. Malar space about a half of diameter of front ocellus . . . . . *Hemitaxonus nigrooralis* (Malaise)

Genus *Strongylogaster* Dahlbom

This genus is represented by 39 species mainly in the temperate zone of the northern hemisphere: 11 species in North America, 8 species in Europe and 26 species in eastern Asia (Naito and Huang 1988). The following five species occur in Taiwan, including a new species and a newly recorded species.

Strongylogaster lineata (Christ)

Strongylogaster lineata: Enslin, 1914, p. 205; Takeuchi, 1941, p. 243; Zhelochovtsev, 1951, p. 152; Benson, 1968, p. 134; Naito, 1980, p. 400.

Specimens examined.—2 ♀ 2 ♂, Tungpu, Nantou Hsien, 10.iv.1965, T. Saigusa; 1 ♂, Meifeng, Nantou Hsiesn, 21.iv.1978, T. Niisato; 2 ♂, Pilushenmu (2200 m), Hualien Hsien, 29.iii.1981, T. Shimomura; 1 ♀, Howangshan, 7.iv.1973, C. C. Lo; 1 ♀, Alishan, Chiayi Hsien, 8.iv.1965, T. Shirozu; 1 ♂, Alishan, 9.iv.1965, Y. Hirashima.

Distribution.—Taiwan, Japan, Korea, Kuriles, Siberia, Caucasus, Turkey, Iran, Europe.

Remarks.—The coloration of the abdomen is significantly variable in both sexes of this widespread species, but it is rather uniform in each sex of specimens from Taiwan. The male abdomen is rufous except for the black basal two segments, and the female abdomen is black with a narrow yellow band on the apical margins of the 2nd to 8th terga.

Strongylogaster fulva Naito and Huang (Fig. 1)

Strongylogaster fulva: Naito and Huang, 1988, p. 41.

Male.—Length, 8.5–9.5 mm. Similar to

female in morphological structure but quite different in coloration: Head and thorax black with labrum, labial and maxillary palpi and tegula yellowish. Legs light brown; coxae black except for extreme apices; trochanters partly brown. Abdomen rufous; propodeum and basal part of 2nd tergite black; 2nd to 5th terga with black mark on lateral sides. Penis valve as in Fig. 1.

Specimens examined.—1 ♂, Kuantaoshan, Miaoli Hsien, 9.iv.1984, C. C. Lo; 1 ♂, Kuantaoshan, 9.v.1984, C. C. Lo; 4 ♂, Howangshan, 7.iv.1984, C. C. Lo; 1 ♀, Sungkang, Nantou Hsien, 4.v.1984, C. C. Lo.

Distribution.—Taiwan, South China.

Remarks.—This species is newly recorded from Taiwan. It was described from females from Tibet and Sichuan, China, by Naito and Huang (1988). The male, which was unknown, is similar to the male of *S. lineata* but is distinguished from the latter by the broadly emarginate clypeus, the shining thorax and propodeum, and the partly rufous 2nd tergite. A female specimen from Taiwan is paler than those from Tibet or Sichuan. The Taiwanese specimen is light brown except for the black 5th to 9th antennal segments and the large black mark on the mesonotal lobe, while the Chinese specimens are dark brown to black with various amounts of orange.

Strongylogaster nantouensis
NEW SPECIES
(Figs. 2, 4, 5)

Female.—Length 9.0 mm. Black; apical margin of labrum, maxillary and labial palpi, tegula and apical margin of abdominal segments yellowish. Legs black to dark brown; apices of fore and mid coxae, apical half of hind coxa, trochanters, apices of fore and mid femora, apical third of hind femur, basal third of fore and mid tibiae and basal ⅔ of hind tibia yellowish. Wings hyaline with apical margins somewhat dark.

Head shining, with close, minute punctures; frontal area with many longitudinal wrinkles; postocellar area smooth. Labrum flat, gently rounded in front. Clypeus nearly flat, shallowly emarginate in front to depth of about ⅙ its medial length. Median fovea represented by small, elongated pit. Lateral fovea open below, with indistinct crest above. Frontal area concave, surrounded by narrow raised carina laterally and by broad, dull carina anteriorly. Interocellar furrow opening out towards front ocellus. Postocellar furrow represented by deep line. Vertical furrow deep, convergent toward front ocellus. Postocellar area convex; breadth : length = 23:13. Vertex with indistinct convex area at outside of lateral ocellus. Post genal carina developed on lower hind margin. Malar space narrow, about ⅓× diameter of front ocellus. Antenna about 2.2× breadth of head; relative lengths of segments about 8: 5:24:23:23:18:17:16:14. Thorax smooth and shining; prescutum with minute and close punctures; lateral and posterior margins of scutellum with several large and separate punctures; prepectus represented by narrow, raised shoulder. Anal cell of fore wing without crossvein. Anal cell of hind wing sessile. Tarsal claw with very small inner tooth. Abdomen (including propodeum) with fine microsculpture. Sawsheath short, not divided at apex in dorsal view, truncate at apex in lateral view (Fig. 4). Saw as in Fig. 5.

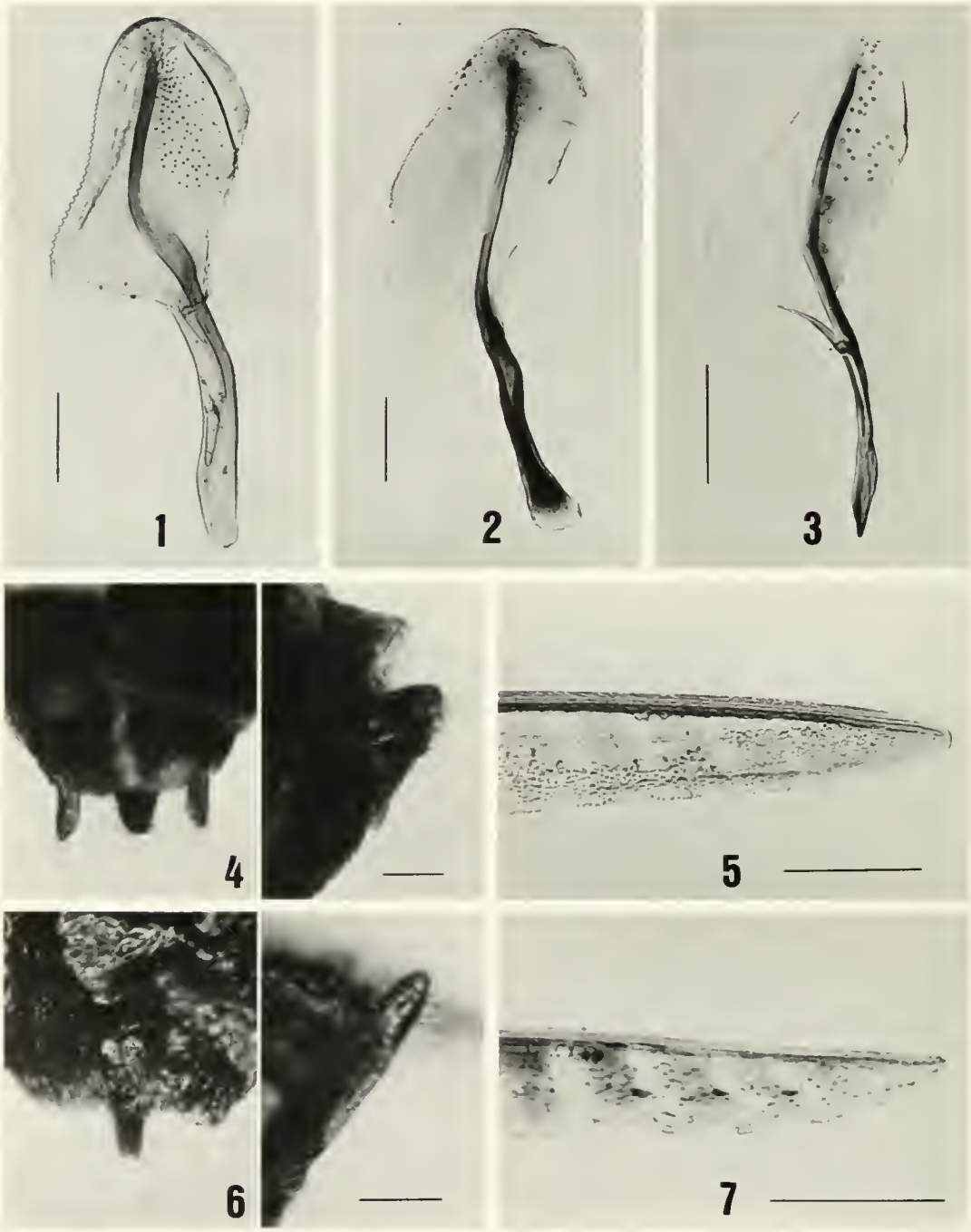
Male. Length, 7.5–8.0 mm. Similar to female except pronotum with upper angle yellow and vertical furrows subparallel with each other. Penis valve as in Fig. 2.

Holotype.—Female, Nanshanchi, Nantou Hsien, 21.iii.1979, A. Shinohara (Deposited in the Entomological Laboratory of Kobe University).

Paratypes.—1 ♂, same locality and date to the holotype; 1 ♂, Nanshanchi, 23.iii.1977, T. Naito; 1 ♂, Meifeng, Nantou Hsien, 8–11.v.1984, K. C. Chou and C. C. Pan; 1 ♂; "Hokuko, Kaminoshimaonsen," Miaoli Hsien, 11.iv.1967, T. Shirozu.

Distribution.—Taiwan.

Remarks.—This new species is similar to *S. soriculatipes* Cresson from North Amer-



Figs. 1–7. Fig. 1, *Strongylogaster fulva*, penis valve. Figs. 2, 4, 5, *Strongylogaster nantouensis*. 2, Penis valve. 4, Sawsheath in dorsal view (left) and in lateral view (right). 5, Saw. Fig. 3, *Strongylogaster formosana*, penis valve. Figs. 6, 7, *Pseudohemitaxonus taiwanus*. 6, Sawsheath in dorsal view (left) and in lateral view (right). 7, Saw. Scale: 0.2 mm in Figs. 1–4, 6; 0.1 mm in Figs. 5, 7.

ica, but the latter species differs from *S. nantouensis* by the yellowish clypeus, yellowish hind femur, dull frontal carina, and broad sawsheath in lateral view.

Strongylogaster formosana (Rohwer) (Fig. 3)

Thrinax formosana Rohwer, 1916, p. 100; Takeuchi, 1941, p. 235.

Male.—Length, 6.5 mm. Similar to female except for entirely black abdomen and anal cell of hind wing with petiole a little longer than breadth of the cell. Penis valve as in Fig. 3.

Specimens examined.—1 ♂, Shitonshan, Miaoli Hsien, 15.iii.1980, T. Tanabe; 1 ♂, Meifeng, Nantou Hsien, 28.v.1975, S. Imasaka; 1 ♂, Tsuifeng (2300 m), Nantou Hsien, 23.iii.1979, A. Shinohara; 1 ♀, Alishan, Chiayi Hsien, 9.v.1922, S. Mori.

Distribution.—Taiwan.

Remarks.—Only two females had been recorded from Taiwan. The male was previously unknown.

Strongylogaster abdominalis (Takeuchi)

Thrinax abdominalis Takeuchi, 1928, p. 42; Takeuchi, 1941, p. 235.

Specimens examined.—1 ♀ 2 ♂, Piananbu-Shikikun, Taipei Hsien, 20.vii.1932, T. Esaki; 1 ♂, Tapingshan, Taipei Hsien, 22.vii.1932, T. Esaki; 1 ♂, Sungkan, Nantou Hsien, 16.iii.1977, A. Shinohara; 1 ♀, Tsuifeng, Nantou Shien, 17.iii.1977, A. Shinohara; 1 ♀ 1 ♂, Alishan (2300 m), Chiayi Hsien, 9.iv.1965, T. Saigusa; 3 ♂, Alishan (2400 m), 5–9.viii.1981, L. Y. Chou and S. C. Lin; 1 ♂, Alishan, 17–20.viii.1982, K. C. Chou and C. C. Pan.

Distribution.—Taiwan.

Genus *Hemitaxonus* Ashmead

Trearea Malaise, 1947, p. 35. New synonym. Type species: *Trearea compressicornis* Malaise. Monotypic.

Canonarea Malaise, 1947, p. 38. New synonym. Type species: *Canonarea albooralis* Malaise. Original designation.

Malaise (1947) described *Trearea* and *Canonarea* as new genera of the Selandrinae and commented that these two genera together with another related genus, *Canonias* Konow, compose a distinct and isolated group in the subfamily. No comments were given on the relationships to other groups. *Canonarea,* however, is quite identical to *Hemitaxonus.* Characters separating *Trearea* from *Canonarea* are the absence of the 1st cubital crossvein in the fore wing and the compressed antenna, but these are considered to be variations within *Hemitaxonus.* The first two genera, therefore, should be included in *Hemitaxonus* as new synonyms.

This genus was represented by 16 species. Four species were recorded from North America (Smith 1969) and 12 species from East Asia, of which only one spreads to Europe (Naito 1971). Three species described by Malaise (1947) as new species of *Canonarea* or *Trearea* are newly included in this genus. Other than the species below, *Hemitaxonus compressicornis* (Malaise), described in *Trearea,* is a new combination. The following three species occur in Taiwan, the last two representing the first records of these species there.

Hemitaxonus formosanus Takeuchi

Hemitaxonus formosanus Takeuchi, 1928, p. 43; Takeuchi, 1941, p. 247.

Specimens examined.—1 ♀, Tapingshan, Taipei Hsien, 24.vii.1932, T. Esaki; 1 ♀, Pahsienshan, Taichung Hsien, 30.viii.1929, K. Takeuchi; 1 ♀ 5 ♂, Sungkang, Nantou Hsien, 18.vii.1972, T. Naito; 1 ♂, Tsuifeng, Nantou Hsien, 18.iii.1977, A. Shinohara; 1 ♂, Tsuifeng (2300 m), 23.iii.1979, A. Shinohara.

Distribution.—Taiwan.

Hemitaxonus albooralis (Malaise), New Combination

Canonarea albooralis Malaise, 1947, p. 38.

Specimens examined.—1 ♀, Meifeng-

Sungkang, Nantou Hsien, 4.v.1978, A. Shinohara; 2 ♀, Meifeng (2150 m), 8–11.v.1984, K. C. Chou and C. C. Pan.

Distribution.—Taiwan, Burma.

Remarks.—Three females from Taiwan are identical with the paratype from Burma in structure and coloration. This is the first record of this species from Taiwan and also outside the type locality, Burma.

Hemitaxonus nigrooralis (Malaise), New Combination

Canonarea nigrooralis Malaise, 1947, p. 39.

Specimens examined.—1 ♀, Lushan (1000 m), Nantou Hsien, 27–31.v.1980, K. S. Lin and L. Y. Chou; 1 ♀, Wusho (1159 m), Nantou Hsien, 6–11.v.1981, K. S. Lin and S. C. Lin; 2 ♀, Tunpu (1200 m), Nantou Hsien, 23–27.vii.1984, K. C. Chou and C. H. Yang; 1 ♀, Lienhwachi, Nantou Hsien, 26.iii.1984, C. C. Lo.

Distribution.—Taiwan, Burma, Himalaya.

Remarks.—This is the first record of this species from Taiwan. I also examined a female specimen from Hymalaya labeled "Panjab, Himalaya, Khajjiar, 23.vi.1965, Tikav leg." These are the first occurrences outside the type locality, Burma.

Genus *Pseudohemitaxonus* Conde

Three species have been described, one from Europe and two from Japan (Naito 1969). The following species represents the first record of this genus from Taiwan.

Pseudohemitaxonus taiwanus New Species (Figs. 6, 7)

Female.—Length, 5.3 mm. Head and thorax black; clypeus, labrum, labial and maxillary palpi, scape, pedicel (with dark band on anterior half), pronotum, tegula and legs (except for hind tarsus infuscate) yellowish. Abdomen dark brown; 2nd to 4th terga pale brown and with yellowish longitudinal line in middle; 2nd to 6th terga with apical margins narrowly and lateral margins broadly yellowish.

Head shining, feebly shagreened, with small punctures and sparse pubescence. Labrum nearly flat, rounded in front. Clypeus gently convex, shallowly emarginate in front to depth of about 1/7 its medial length. Median fovea indistinct and lateral fovea punctiform. Frontal area represented by feebly raised platform, not clearly defined. Interocellar and postocellar furrows absent. Vertical furrow represented by shallow line, somewhat convergent toward apex. Postocellar area nearly flat; breadth : length = 15:7. Malar space about 2/5× diameter of front ocellus. Postgenal carina developed on lateral side. Antenna filiform, about 2.1× breadth of head; relative lengths of segments about 6:5:24:24:20:15:15:12:14. Thorax shining and smooth; mesonotal middle lobe and lateral lobes with small and close punctures; pronotum, scutellum and mesepisternum with sparse and fine punctures. Posttergite large, about 1.5 times as wide as scutellum. Prepectus defined by distinct suture. Anal cell of fore wing with subcrect crossvein; 1st cubital crossvein absent; vein Rs+M strongly curved toward stigma. Anal cell of hind wing with petiole about 1.5× greatest breadth of cell. Inner front tibial spur slender, slightly bifid at apex. Tarsal claw with very small inner tooth. Abdomen feebly reticulate throughout. Propodeum deeply and broadly excised. Sawsheath slender, not bifid at apex (Fig. 6). Saw as in Fig. 7.

Male.—unknown.

Holotype.—Female, Meifeng, 2150 m, Nantou Hsien, 19–21.iv.1983, K. C. Chou and S. P. Huang (Deposited in the Taiwan Agricultural Research Institute).

Distribution.—Taiwan.

Remarks.—This new species resembles *P. dryopteridis* Naito from Japan but is easily distinguished from the latter by the frontal area which is not surrounded by a carina, the clearly defined prepectus, and the very

small but distinct inner tooth on the tarsal claw.

Acknowledgments

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A REVISION OF THE SHORE-FLY GENUS *DIPHUIA* CRESSON (DIPTERA: EPHYDRIDAE)

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Abstract.—*Diphuia* Cresson, a New World genus of shore flies, is revised and found to be close phylogenetically (the sister group) to the lineage giving rise to *Allotrichoma* Becker, including *Pseudohecamede* Hendel. Although four species (*D. anomala* Cresson, *D. nasalis* Wirth, *D. nitida* Sturtevant and Wheeler, and ***D. zatwarnickii***, new species (Jamaica) are recognized, the second and third are very similar and may prove to be conspecific when adequate material of *D. nitida* is available. Characters of the male postabdomen and terminalia are described and illustrated.

Key Words: Ephydridae, shore flies, *Diphuia*, revision, systematics

While conducting field work on several cays within the Stann Creek District of Belize, I found a tiny, black-colored shore fly that is associated with mangrove peat. The peat, which is exposed at low tide, is shaded during most of the day beneath the dense canopy of well-developed fringe red mangrove (*Rhizophora mangle* L.). The specimens did not occur on peat that is the substrate for scrub or dwarf red mangrove and where little or no shade is provided. Determining the identity of this species, which is less than two mm in length, has led to this revision of *Diphuia* Cresson, the genus to which the species has been assigned. In addition to determining the identity of the specimens from Belize, the other specific purposes of this revision are to provide the first illustrations of the male terminalia and to determine the phylogenetic position of *Diphuia*, which Cresson (1944) suggested was related to *Allotrichoma* Becker in the tribe Atissini.

Shore flies of the genus *Diphuia* are anomalies among atissines in being mostly black, lacking dense vestiture of gray to brown microtomentum, and having a distinctively marked face that is black with silvery white, microtomentose lines. The facial markings of microtomentum are similar to specimens of *Discocerina nitida* Cresson (tribe Discocerinini) and several genera of the tribe Gymnomyzini. The superficial resemblance of this genus to discocerines or gymnomyzines prompted Cresson to formulate the generic name *Diphuia*, which is a Latin transliteration of Greek words meaning double nature. Although similar to genera in other tribes, the genus is related most closely to *Allotrichoma*, as Cresson concluded in the original description, and the similarities noted are apparently the result of convergences.

When Cresson (1944) originally proposed *Diphuia* he included only the type species, *D. anomala* Cresson, which was described in the same paper. Two years later, Cresson again treated *Diphuia* and its type species in his synopsis of Neotropical Psilopinae (= Gymnomyzinae). The genus then remained unstudied for nearly a decade, which is not surprising in view of their diminutive size,

restricted distribution, and rarity in collections. Sturtevant and Wheeler (1954) wrote the concluding part for Cresson's synopses of Nearctic shore flies, following the latter's death, and described *D. nitida* from a single specimen that was collected near New York City. Two years afterwards, Wirth (1956) reviewed the shore flies of the Bahamas and described a third species, *D. nasalis*. Aside from catalogs of the Nearctic and Neotropical Regions (Wirth 1965, 1968, respectively), no further work has been published on *Diphuia*. Nothing is known of the immature stages, no key is available, and the structures of the male terminalia have not been investigated, described, or illustrated.

Methods.—The terminology and methods used in this study were explained previously (Mathis 1986a, b). Because of the small size of specimens, study and illustration of the male terminalia required the use of a compound microscope. To better assure effective communication about structures of the male terminalia, I have adopted the terminology of other workers in Ephydridae (see references in Mathis 1986b). Usage of these terms, however, should not be taken as an endorsement of them from a theoretical or morphological view over alternatives that have been proposed (Griffiths 1972, McAlpine 1981). Rather, I am deferring to tradition until the morphological issues are better resolved.

Two venational ratios are used commonly in the descriptions and are defined here for the convenience of the user (ratios are averages of three specimens).

1. Costal vein ratio: the straight line distance between the apices of R_{2+3} and R_{4+5}/ distance between the apices of R_1 and R_{2+3}.

2. M vein ratio: the straight line distance along M between crossveins (dm-cu and r-m)/distance apicad of crossvein dm-cu.

Most of the specimens used in this study, a total of 225, are housed in the National Museum of Natural History (USNM), Smithsonian Institution. Prior to my tenure at the Smithsonian, W. W. Wirth had accumulated several specimens of what appeared to be the same tiny fly. His collections from Jamaica and Dominica are especially noteworthy in that regard. I also examined collections of the Academy of Natural Sciences of Philadelphia (ANSP), the American Museum of Natural History (AMNH), and the University of Texas (UTA).

Diphuia Cresson

Diphuia Cresson, 1944: 4. Type species: *Diphuia anomala* Cresson, 1944, by original designation; 1946: 138, 140 [note, key].—Sturtevant and Wheeler, 1954: 248 [notes].—Wirth, 1956: 4 [discussion of species]; 1968: 5 [Neotropical catalog].

Diagnosis.—Mostly black, subshiny to shiny, microtomentum usually sparse; small shore flies, length 1.35 to 1.80 mm.

Head: Wider than high; face width-to-head width ratio 0.28; frons black, mostly unicolorous, lacking distinctively colored ocellar triangle; frons wider than long, frontal length-to-width ratio 0.58; frontal vestiture variable; ocellar seta well developed, inserted slightly in front of alignment of anterior ocellus and at about the same distance apart as between posterior ocelli; pseudopostocellar setae usually well developed, length subequal to ocellar setae, proclinate, slightly divergent; 1 reclinate and 1 proclinate fronto-orbital seta present, reclinate seta inserted slightly anteromediad of proclinate seta; both inner and outer vertical setae present; ocelli arranged to form isosceles triangle, with distance between posterior ocelli larger than between anterior ocellus and either posterior ocellus. Antenna exerted; pedicel with well-developed, proclinate, dorsal seta; aristal length subequal to antennal length and bearing 4–5 dorsal rays, with basal 3 rays longer than apical 1–2, the latter subequal. Eye apparently bare of microsetulae (using a stereomicroscope). Face black in both sexes and with silvery white, microtomentose antennal grooves and with

2 lines, sometimes irregular, paralleling parafacials, these and similarly invested and colored ventral margin (microtomentum sometimes interrupted at middle) form a facial triangle that has a small microtomentose area below facial prominence; face not carinate between antennal bases but slightly, conically protrudent at middle (best seen in lateral view); ventral facial margin shallowly emarginate; face bearing 2 facial setae, the dorsal seta very slightly larger, both inserted near parafacials; parafacials densely microtomentose, silvery white; clypeus very sparsely microtomentose, black; palpus blackish brown to black; mouthparts not geniculate, labella shorter than mediproboscis.

Thorax: Generally black, vestiture of microtomentum variable with species, although generally sparse; pleural areas lacking stripes of distinctly colored microtomentum. Chaetotaxy with mesonotal setae poorly developed except for those at posterior margin; mesonotal setulae numerous and not arranged in well-defined setal tracks; prescutellar acrostichal setae much larger than other acrostichal setulae and more widely set apart; only 1 dorsocentral seta, inserted posteriad; intra-alar setulae irregularly seriated; presutural seta well developed, length subequal to notopleural setae; 2 scutellar setae and scutellar disc with sparse, scattered setulae; postpronotal seta 1; postalar seta 1; notopleural setae 2, insertion of posterior seta elevated dorsally above anterior one; anepisternal setae 2, inserted along posterior margin; katepisternal seta well developed, conspicuous. *Wing:* membrane mostly hyaline to very slightly milky white; veins behind costa pale, usually yellowish to yellowish brown; vein R_{2+3} extended well beyond level of crossvein dm-cu, 2nd costal section at least 1½ times longer than 3rd section; alular marginal setulae short, less than ½ alular height. *Legs:* femora black; tibiae dark basally, concolorous with femora, apices yellowish.

Abdomen: Fifth segment of male well sclerotized, elongate, not normally visible from a dorsal view, usually retracted within 4th segment; 5th tergum and sternum of male united anteriorly to form a complete annulus. Male terminalia as follows: cercus rod shaped, bearing 2–3 conspicuously longer setae at ventral margin; surstylus well developed, well sclerotized, and conspicuous, length as long as cercus.

Distribution.—New World. Temperate to tropical zones, in North America along the east coast (New York south to Florida) and the Caribbean to Colombia and Eucador in South America.

Phylogenetic relationships.—*Diphuia* is related to a group of taxa (*Allotrichoma* Becker, *Eremotrichoma* Soika, *Pseudohecamede* Hendel, and *Hecamede* Haliday) within the tribe Atissini that is characterized by having very sparse or lacking microsetulae on the compound eyes; a conically prominent face (degree of development varies) that is emarginate ventrally and with the clypeus exposed in the emargination; oral opening and clypeus narrow; area surrounding crossvein dm-cu not infuscate; the apex of the wing broadly rounded, not pointed at the apex of vein R_{4+5}; fifth tergum of male retracted within the enlarged fourth, usually not visible; and cerci with elongate setulae at ventral margin. *Diphuia* appears to be the sister group to the lineage giving rise to taxa closely related to *Allotrichoma* sensu lato, including *Pseudohecamede.* This relationship is evidenced by the characters noted previously, especially the retracted fifth tergum of the male, which is moderately elongate, almost tubular. Although related and similar to this group, *Diphuia* may be distinguished as follows (characters indicated by an asterisk are autapomorphies that corroborate the monophyly of *Diphuia*): *coloration very dark, usually black; *microtomentum of head and thorax generally sparse, giving a subshiny to faintly dull appearance; facial coloration of male and females similar, lacking sexual dimorphism; face, although slightly pro-

trudent medially (best seen in profile), not acutely pointed in lateral view; *face with silvery microtomentose markings, antennal grooves, 2 vertical lines, ventral margin, an area below the facial prominence, and parafacials; presutural and prescutellar setae well developed; *pleural region lacking a stripe or stripes; 5th segment of male well sclerotized and its tergum moderately enlongate; *5th tergum and sternum of male united anteriorly to form a complete annulus; and male genitalia with distinct, well-sclerotized, elongate surstyli. The placement of *Diphuia* as the sister group to the lineage of *Allotrichoma* sensu lato follows Cresson's original assessment. The evidence supporting this relationship is not strong, however, and *Diphuia* could be related to *Hecamede*.

Two species groups are evident within *Diphuia*, each comprising two species: *D. anomala* Cresson and *D. zatwarnickii*, a new species that is described below; and *D. nitida* and *D. nasalis*. For species in the former group, I have found that characters of the male terminalia only are adequate to distinguish between the species. In the second group, the degree of microtomentum on the frons may be a distinguishing character, although that character is questionable (see "Remarks" under *D. nitida*).

Discussion.—Two shore-fly species (*Discocerina quadripectinata* (Becker) and *Allotrichoma argentipraetextum* Lamb) that are now or perhaps should be assigned to *Allotrichoma* and related genera and that are dark colored are not closely related to *Diphuia* (Zatwarnicki, in litt.).

Nothing is known about the immature stages or natural history of any of the species included in *Diphuia*.

Key to Species of *Diphuia*

1. Mesofrons bare of microtomentum, shiny (New York) ..... *D. nitida* Sturtevant and Wheeler
– Mesofrons mostly densely microtomentose, at most with small shiny area immediately before anterior ocellus (southeastern USA and Neotropics) 2
2. Mesonotum thinly invested with microtomentum, subshiny; anepisternum with anteroventral ⅓–½ bare, shiny black, otherwise with thin investment of whitish gray microtomentum ..... *D. nasalis* Wirth
– Mesonotum moderately densely microtomentose, golden brown; anepisternum almost entirely invested with whitish gray microtomentum 3
3. Surstyli long and narrow, length subequal to that of cercus (Fig. 3); gonite with pointed posteroventrally; aedeagus only moderately curved apically ..... *D. anomala* Cresson
– Sturstyli moderately short and robust (Fig. 18), length shorter than cercus; gonite with posteroventral portion broadly bifurcate; aedeagus more curved apically, point oriented anteriorly ..... *C. zatwarnickii*, new species

***Diphuia anomala* Cresson**
Figs. 1–7

Diphuia anomala Cresson, 1944: 4; 1946: 138 [review].—Wirth, 1968: 5 [Neotropical catalog].

Description.—Small shore flies, length 1.60 to 1.80 mm.

Head: Frons moderately invested with brownish microtomentum, microtomentum sparse or lacking on 2 small areas laterad of posterior ocelli and 2 spots along the anterior margin.

Thorax: Mesonotum densely invested with brownish to golden brown microtomentum, especially medially, along posterior portion of scutum and scutellum; anepisternum with fine investment of whitish microtomentum. Wing with costal vein ratio 0.50; M vein ratio 0.41.

Abdomen: 5th tergum (Figs. 1, 2) almost as high as long, anterior margin in dorsal view with deep, broadly V-shaped emargination (Fig. 2), posterior margin with sparse setae; 5th sternum clearly divided into 2 broad sternites that are connected only anteroventrally (Fig. 1). Male terminalia (Figs. 3–7) as follows: epandrium bulbous, shiny, in lateral view almost as wide as high (Fig. 3); surstylus long, narrow, parallel sided, width and length subequal to that of cercus, apex angulate, pointed anteriorly, and bear-

ing a few setulae (Fig. 3); gonite broad basally, with posteriorly extended process sheathing aedeagus, posterior apex of gonite curved anteroventrally (Figs. 4, 5); aedeagal apodeme triangular in lateral view (Figs. 5, 7), narrowly produced dorsally; aedeagus in lateral view broad, thumblike, produced posteroventrad to a ventral point, in dorsal view becoming wider apically, apex broadly rounded (Figs. 5, 7); hypandrium in ventral view longer than wide, anterior margin with a small, anterior process (Figs. 5, 6).

Type material.—The holotype male is labeled "Monte Lirio[,] PANAMA[,] RCShannon[,] 1V.6.23 [6 Apr 1923]/♂/ TYPE DIPHUIA ANOMALA ♂ E.T. Cresson, Jr. [red, species name and ♂ handwritten]; TypeNo 70450 USNM [red, number handwritten]." The holotype is point mounted, is in good condition (the right first flagellomere is missing), and is deposited in the USNM. The allotype and several paratypes are also deposited in the USNM.

Other specimens examined.—*COLOMBIA.* Rio Raposo (light trap), Jan 1964, V. H. Lee (1 ♂; USNM). *ECUADOR.* Los Ríos Province. Guare, Aug 1955, J. R. Levi-Castillo (6 ♂, USNM). Manabi Province. Camarones, 9 Sep 1955, J. R. Levi-Castillo (1 ♂; USNM); Estero Balsa, 9 Sep 1955, J. R. Levi-Castillo (13 ♂, 3 ♀; USNM); La Palma, Aug 1955, J. R. Levi-Castillo (1 ♂; USNM). *EL SALVADOR.* Laguna de Zapotitan, Dec 1953, W. B. Heed (1 ♀; UTA). *PANAMA.* Canal Zone: Balboa, Feb 1958, M. R. Wheeler (1 ♂; UTA), Monte Lirio, 6 Apr 1923, R. C. Shannon (29 ♂, 19 ♀; ANSP, USNM); Pedro Miguel, 10 Apr 1923, R. C. Shannon (4 ♂, 1 ♀; USNM). Panama: Darién: Sabanas, 20 Apr 1923, R. C. Shannon (4 ♂, 2 ♀; USNM). Panama City, 5 Apr 1923, R. C. Shannon (2 ♀; ANSP, USNM).

Distribution.—Colombia, Ecuador, El Salvador, and Panama.

Remarks.—This is the type species of *Diphuia.* It is very similar externally to *D. zatwarnickii* and can be distinguished only by reference to structures of the male terminalia (see "Remarks" under *D. zatwarnickii* and couplet 3 of the key). From *D. nasalis* and *D. nitida* it may be distinguished by the following characters: frons and mesonotum invested moderately densely with brownish to golden brown microtomentum; anepisternum invested with fine, grayish to whitish microtomentum, anteroventral portion not bare, shiny; second costal section long, costal vein ratio 0.50; and several characters of the male terminalia (see description and figures).

Diphuia nasalis Wirth

Figs. 8–15

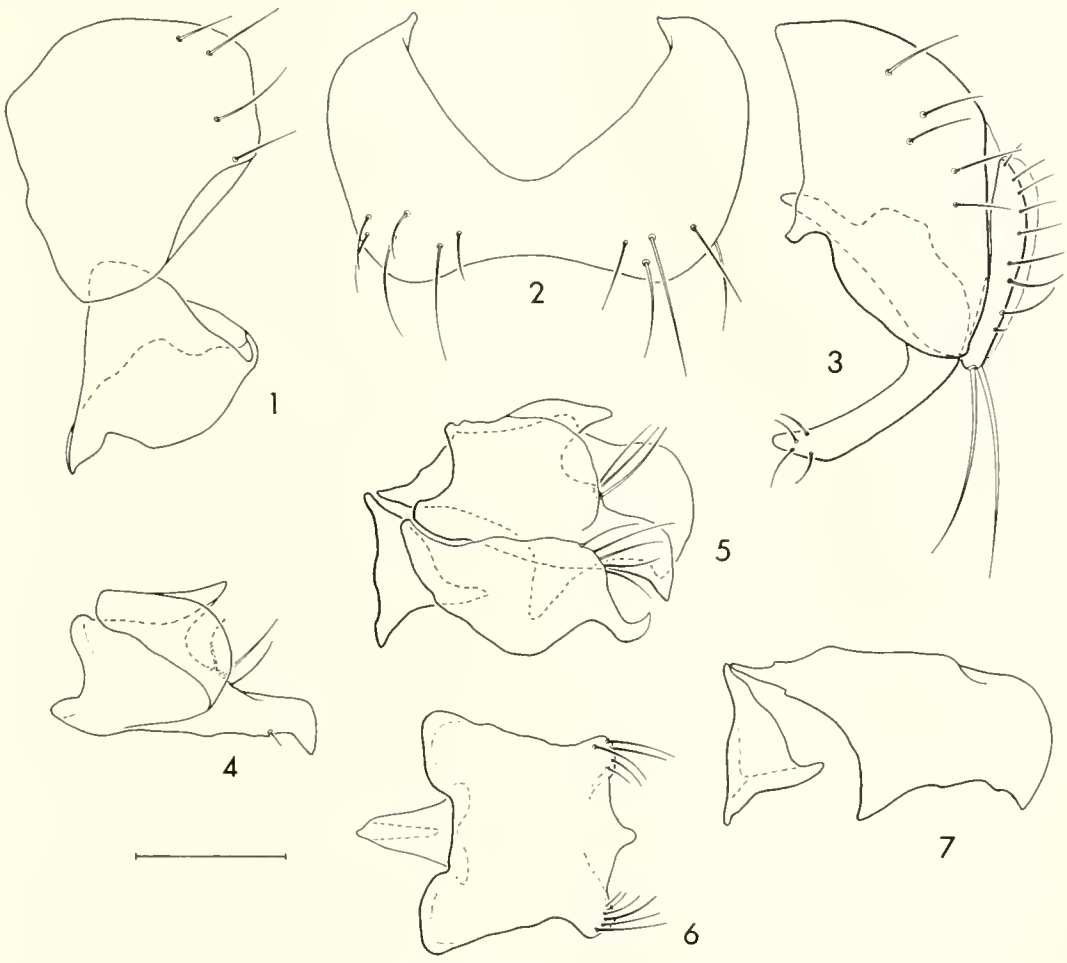
Diphuia nasalis Wirth, 1956: 3; 1968: 5 [Neotropical catalog].

Description.—Small shore flies, length 1.35 to 1.75 mm.

Head: Frons sparsely invested with fine brownish microtomentum, microtomentum becoming sparser or lacking on 2 small areas laterad of posterior ocelli, 2 spots along the anterior margin, and sometimes a small spot in front of the anterior ocellus.

Thorax: Mesonotum sparsely invested with fine brownish to golden brown microtomentum, mostly subshiny to shiny; anepisternum with anteroventral ⅓ to ½ bare of microtomentum, shiny, posterodorsal portion invested with fine, grayish microtomentum. Wing with costal vein ratio 0.58; M vein ratio 0.40.

Abdomen: 5th tergum with anterior margin essentially straight, at most very shallowly arched anteriorly (Fig. 9); 5th sternum undivided, as a narrow band connected dorsally with anteroventral portion of 5th tergum (Fig. 8). Male terminalia (Figs. 10–15) as follows: epandrium narrow in lateral view, much higher than wide (Fig. 10); surstylus as long as cercus but almost twice its width, broadly rounded apically (Fig. 10); gonite in lateral view parallelogram-shaped, posterior angles produced into pointed processes, posteroventral process sinuate (Figs. 11, 12); aedeagal apodeme rounded anter-

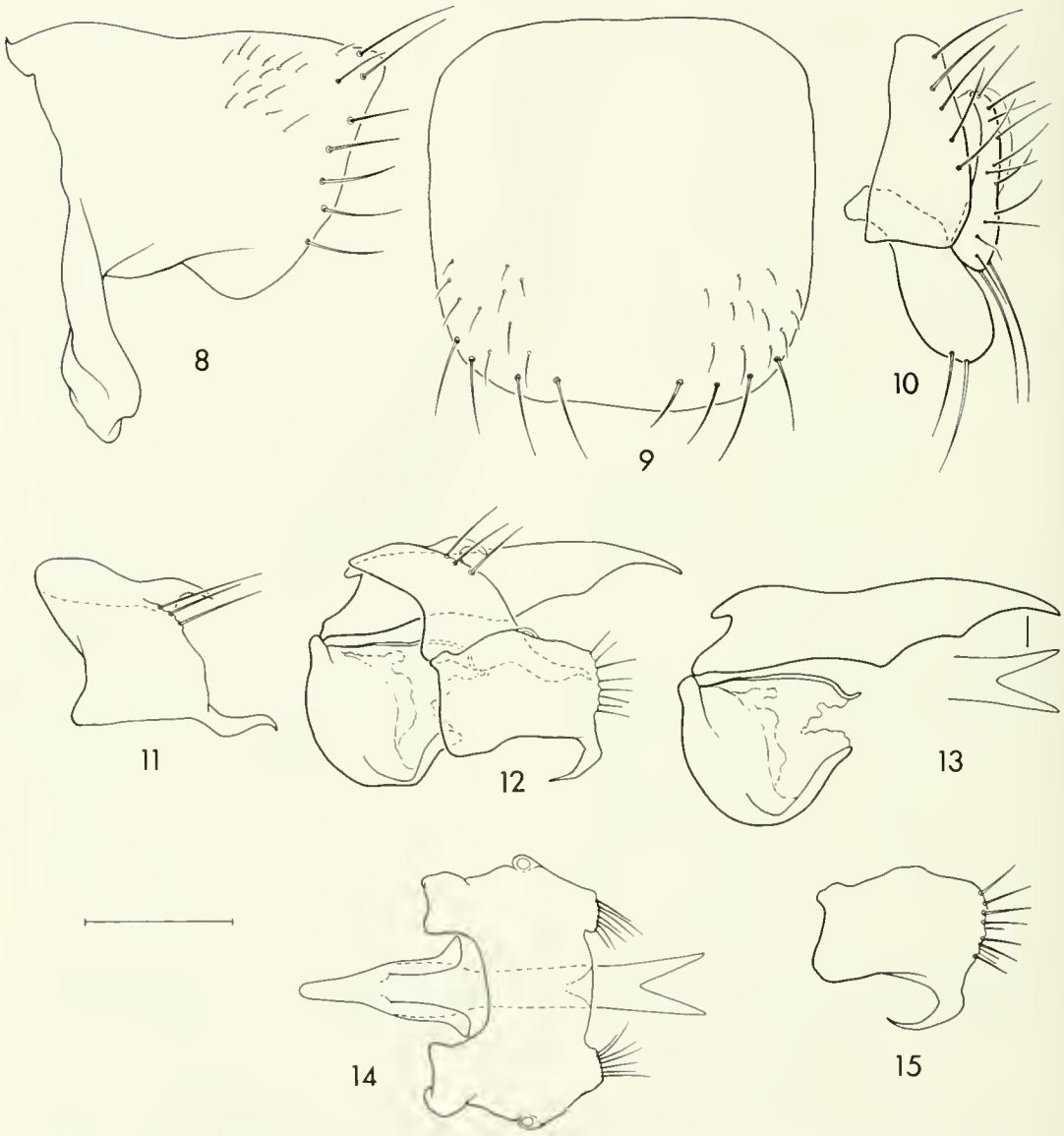


Figs. 1–7. *Diphuia anomala.* 1, 5th tergum and sternum, lateral view. 2, 5th tergum, dorsal view. 3, Male terminalia (epandrium, cercus, surstyli), lateral view. 4, Gonite, lateral view. 5, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 6, Hypandrium and aedeagal apodeme, ventral view. 7, Aedeagus and aedeagal apodeme, lateral view. Scale bar = 0.1 mm.

oventrally (Figs. 12, 13); aedeagus acutely pointed apically, in dorsal or ventral view bifurcate apically (Figs. 12–14); hypandrium in ventral view wider than long, anterior margin shallowly arched anteriorly (Figs. 12, 14, 15).

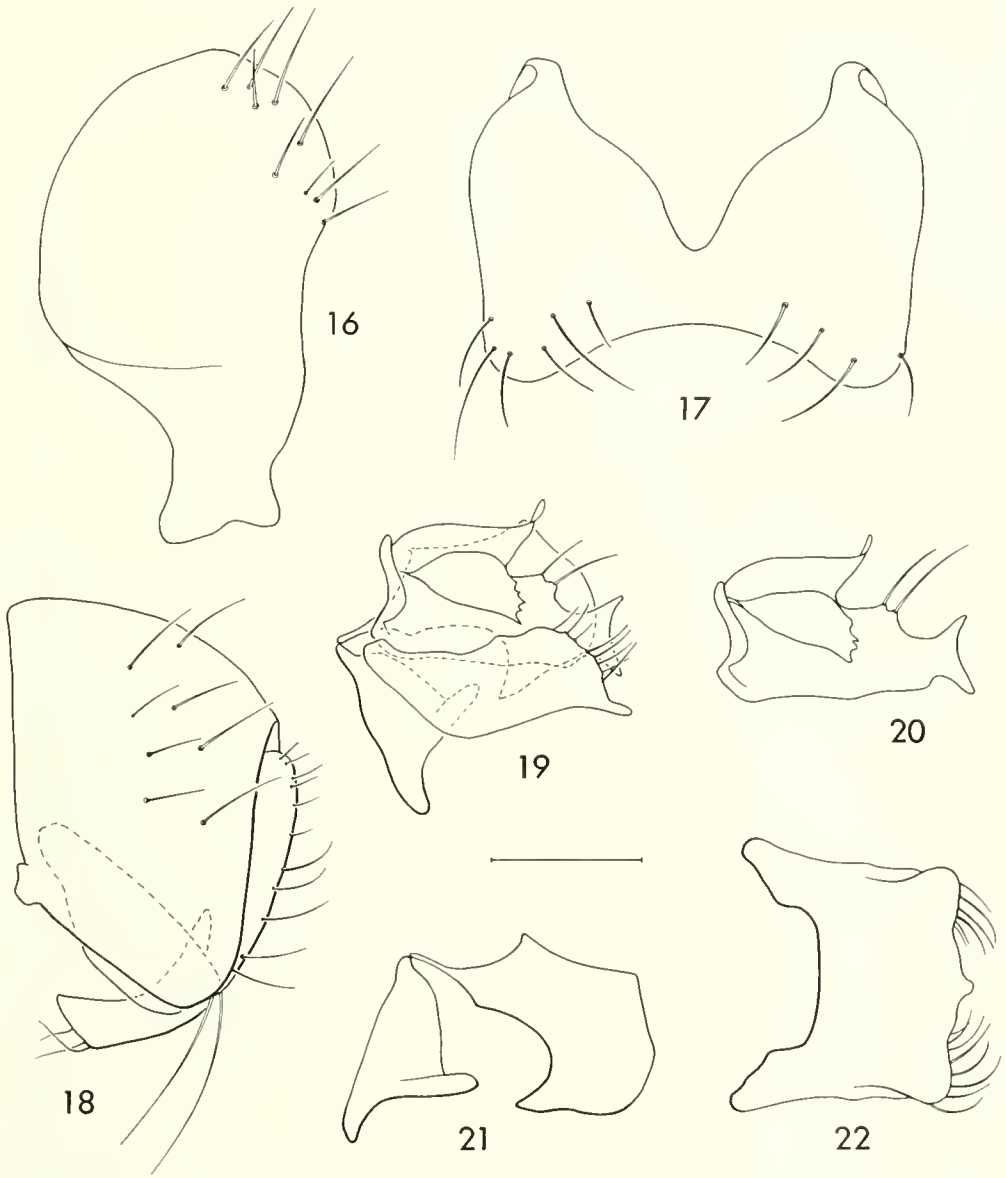
Type material.—The holotype female is labeled "Long Island[,] Deadman's Cay[,] March 11, 1953/Van Voast—A.M.N.H. Bahama Isls. Exped Coll. E. B. Hayden/♂/♂HOLOTYPE Diphuia nasalis W. W. Wirth [red, gender and species name handwritten]." The holotype is point mounted, is in good condition (tip of right wing folded back on itself), and is deposited in the AMNH. Although the holotype was listed as a male (Wirth 1956: 4) and the specimen is so marked, it is a female.

Other specimens examined.—*BAHAMAS.* Crooked Island, Landrail Point, 5 Mar 1953, E. B. Hayden, L. Giovannoli (1 ♀; AMNH); Exuma Cays, Staniard Bay, 13 Jan 1953, E. B. Hayden (1 ♀; AMNH); Long Island, Deadman's Cay, 11 Mar 1953, E. B. Hayden (2 ♂; AMNH, USNM). *BELIZE.* Stann Creek District: Bread and Butter Cay,



Figs. 8–15. *Diphuia nasalis*. 8, 5th tergum and sternum, lateral view. 9, 5th tergum, dorsal view. 10, Male terminalia (epandrium, cercus, surstyli), lateral view. 11, Gonite, lateral view. 12, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 13, Aedeagus and aedeagal apodeme, lateral view. 14, Hypandrium, aedeagal apodeme, and aedeagus, ventral view. 15, Hypandrium, lateral view. Scale bar = 0.1 mm.

25 Mar 1988, W. N. Mathis (5 ♂, 1 ♀; USNM); Glover's Reef (Long Cay, Middle Cay, Northeast Cay, Southwest Cay), 26–28 Jul 1989, W. N. Mathis (29 ♂, 12 ♀; USNM); Man of War Cay, 8–15 Nov 1987, W. N. & D. Mathis (7 ♂, 4 ♀; USNM); Twin Cays (West Bay), 22 Mar 1988, W. N. Mathis (1 ♂, 1 ♀; USNM); Wee Wee Cay, 24–25 Mar 1988, 21 Jul 1989, W. N. Mathis (5 ♂; USNM). Six Belize, 1959, N. L. H. Krauss (1 ♂; USNM). *BERMUDA*. Hamilton Parish. Shelly Bay, 20 Nov 1987, D. J. Hilburn,



Figs. 16–22. *Diphuia zatwarnickii*. 16, 5th tergum and sternum, lateral view. 17, 5th tergum, dorsal view. 18, Male terminalia (epandrium, cercus, surstyli), lateral view. 19, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 20, Gonite, lateral view. 21, Aedeagus and aedeagal apodeme, lateral view. 22, Hypandrium, ventral view. Scale bar = 0.1 mm.

N. E. Woodley (2 ♀; USNM). *JAMAICA*. Falmouth (bay shore), 1 Mar 1969, W. W. Wirth (1 ♂; USNM); Milk River Bath (mangroves), 11 Mar 1970, T. Farr, W. W. Wirth (5 ♂, 1 ♀; USNM); Negril Beach (rocky shore), 12 Mar 1970, W. W. Wirth (1 ♂; USNM); Runaway Bay (bay shore), 16–28 Feb 1969, W. W. Wirth (3 ♂; USNM). *UNITED STATES*. Florida. Monroe Co., Bahia Honda Key (seashore), 11 Apr 1970, W. W. Wirth (4 ♂, 3 ♀; USNM); Big Pine Key, 11 Apr–30 Dec 1954, 1970, H. V. Weems (1

♂, 1 ♀; USNM); Long Key, 23 Jun 1953, M. R. Wheeler (1 ♂; UTA); Saddlebunch Keys, 29 Dec 1953, H. V. Weems (1 ♂, 1 ♀; USNM). North Carolina. Onalow Co., Ashe Island, 11 Aug 1975, J. C. Dukes (1 ♀; USNM).

Distribution.—Bahamas, Belize, Bermuda, Jamaica, and USA (Florida, North Carolina).

Natural history.—The vast majority of specimens from the Belizean cays were collected by sweeping just above mangrove peat that is well shaded most of the day. A few specimens, apparently feeding, were collected on flowers. The association with mangrove peat must be opportunistic, as the species occurs in areas where mangrove does not now exist.

Remarks.—This species is distinguished from congeners, especially *D. anomala* and *D. zatwarnickii,* by the sparsely microtomentose mesofrons (although not shiny as in *D. nitida*); the subshiny mesonotum that is very thinly invested with fine microtomentum; the shiny anteroventral one-third to one-half of the anepisternum; and several characters of the male terminalia (see description and figures).

Diphuia nitida Sturtevant and Wheeler

Diphuia nitida Sturtevant and Wheeler, 1954: 248.—Wirth, 1965: 737 [Nearctic catalog].

Description.—Small shore flies, length 1.60 mm.

Head: Frons, except for fronto-orbits, bare, shiny, especially mesofrons and frontal triangle; fronto-orbits invested with brown microtomentum; frontal triangle chestnut brown, mesofrons otherwise black.

Thorax: Mesonotum sparsely microtomentose, subshiny to shiny, black; anepisternum mostly shiny, posterodorsal angle with some grayish to whitish microtomentum.

Type material.—The holotype ♀ is labeled "Dougl[t]s[t]on[,] L[ong]. I[sland]., N[ew]. Y[ork].[,] Au[gust]. 17, [19]52/HOLOTYPE Diphuia nitida Stvt & Whlr [pink]/TYPE 6695 [dark pink; number handwritten]." The holotype is point mounted, is in poor condition (the antennae and several setae are missing and the left side of the body and wings are covered partially with glue), and is deposited in the ANSP (6695). Sturtevant and Wheeler stated that this specimen is a male, but is clearly a female.

Distribution.—USA. New York: Long Island, Douglaston (just within the city limits of New York City).

Remarks.—This species is very similar to, and may be conspecific with, *D. nasalis.* Resolution of this question will depend on collection and study of additional material, especially males, from the type locality or a locality nearby. At present, the only known specimen of this "species" is the female holotype, which, as noted earlier, is in poor condition, making it impossible to ascertain its identity with certainty. I recognize the holotype as being different and possibly representing a separate species mostly because the few external features that are discernable, especially those of the head, are not within the variation among specimens of *D. nasalis* that I have studied. The shinier frons of the holotype appears to be unique. Furthermore, the distance between New York, which is the type locality of this species, and the nearest locality where *D. nasalis* is known to occur (North Carolina) is several hundreds of miles. As these populations are somewhat disjunct and are apparently different, I am provisionally recognizing them as representing separate species. If the populations prove to be conspecific, *D. nitida* is the senior synonym.

Diphuia zatwarnickii, New Species
Figs. 16–22

Description.—Small shore flies, length 1.40 to 1.90 mm.

Head: Frons moderately invested with brownish microtomentum, microtomentum sparse or lacking on 2 small areas la-

terad of posterior ocelli and 2 spots along the anterior margin.

Thorax: Mesonotum densely invested with brownish to golden brown microtomentum, especially medially, along posterior portion of scutum and scutellum; anepisternum with fine investment of whitish microtomentum. Wing with costal vein ratio 0.52; M vein ratio 0.42.

Abdomen: 5th tergum (Figs. 16, 17) about as high as long, anterior margin in dorsal view with deep, broadly V-shaped emargination (Fig. 17), posterior margin with sparse setae; 5th sternum clearly divided into 2 broad sternites that are connected only anteroventrally (Fig. 16). Male terminalia (Figs. 18–22) as follows: epandrium bulbous, shiny, in lateral view almost as wide as high (Fig. 18); cercus cylindrical; surstylus moderately long and narrow, parallel sided, width subequal to that of cercus but length shorter, apex angulate, pointed anteriorly, and bearing a few setulae (Fig. 18); gonite broad basally, with posteriorly extended process sheathing aedeagus, posterior apex of gonite bifurcate (Figs. 19, 20); aedeagal apodeme triangular in lateral view (Figs. 19, 21), narrowly produced dorsally; aedeagus in lateral view broad, thumblike, curved posteroventrad to an anteroventral point, in dorsal view becoming wider apically, apex broadly rounded (Figs. 19, 21); hypandrium in ventral view longer than wide, anterior margin with a small, anterior process (Fig. 22).

Type material.—The holotype male is labeled "JAMAICA 5mi.E.Negril 13March 1970 W. W. Wirth fresh marsh." The allotype female and three other paratypes (2 ♂, 1 ♀; USNM) bear the same label data as the holotype. Other paratypes are from: *DOMINICA.* Cabrit Swamp, 22–25 Mar 1965, W. W. Wirth (6 ♂, 2 ♀; USNM); Woodford Hill, 27 Feb 1965, W. W. Wirth (2 ♂; USNM). *JAMAICA.* Kingston, Fresh River, 24 Feb 1969, W. W. Wirth (8 ♂, 5 ♀; USNM); Milk River Bath, 11 Mar 1970, T. Farr, W. W. Wirth (7 ♂, 4 ♀; USNM); Rio Bueno, 21 Feb 1969, W. W. Wirth (1 ♂; USNM); Savanna La Mar, 13 Mar 1970, W. W. Wirth (2 ♂; USNM). The holotype is double mounted (minute nadel in polyporus block), is in excellent condition, and is deposited in the Smithsonian Institution (USNM).

Distribution.—West Indies: Dominica and Jamaica.

Etymology.—This species is named for Tadeusz Zatwarnicki, who first brought this species to my attention and who has contributed significantly to the study of shore flies.

Remarks.—This species is distinguished from *D. nasalis* and *D. nitida* by the sparsely microtomentose mesofrons; the subshiny mesonotum that is very thinly invested with fine microtomentum; the shiny anteroventral one-third to one-half of the anepisternum; and several characters of the male terminalia. This species is distinguished from *D. anomala* by characters of the male terminalia: especially the shorter, more robust surstyli; the gonite that is broadly bifurcate posteroventrally; and the more apically curved aedeagus (see description and figures).

Acknowledgments

I am grateful for the assistance in the field from Candy Feller, Holly Williams, and Dianne Mathis. For the opportunity to examine specimens housed in their collections, I thank David Grimaldi and Julian Stark (AMNH) and Donald Azuma (ANSP). For critically reviewing a draft of this paper, I thank Allen Norrbom, Norman Woodley, Willis Wirth, and Tadeusz Zatwarnicki. The illustrations were skillfully inked by Elaine R. S. Hodges.

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92(4), 1990, pp. 757–759

NOTE

Dispersal of the Southern Green Stink Bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae), by Hurricane Hugo

Nezara viridula (L.) (Heteroptera: Pentatomidae), called the southern green stink bug in the U.S., is native to the Ethiopian Region (Jones 1988, Ann. Entomol. Soc. Am. 81: 262–273; Hokkanen 1986, Ann. Entomol. Fenn. 52: 28–31), but now is a worldwide pest of a multitude of crops (Todd 1989, Annu. Rev. Entomol. 34: 273–292). Range expansion of *N. viridula* is ongoing although its distribution has long been cosmopolitan, including tropical areas of Asia, northern Africa, Europe, and the Americas by the 18th century (Hokkanen 1986). Most recently, the southern green stink bug has invaded the Sacramento Valley in California (Hoffmann, Wilson, and Zalom 1987, Calif. Agric. 41: 4–6).

On October 4, 1989, an adult *N. viridula* female was collected by sweep net in a soybean plot at the South Farm, Agricultural Research Center, Beltsville, Maryland. This locale is over 600 km north of the normal range for the southern green stink bug in the eastern U.S. (Jones and Sullivan 1981, Environ. Entomol. 10: 409–414); ". . . records for more northern states, like Ohio, New York, and Virginia, probably are adventitious occurrences" (Froeschner, *In* Henry and Froeschner 1988, Catalog of the Heteroptera, or True Bugs, of Canada and the Continental United States, E. J. Brill: 588). Extensive sweeping of the same and adjacent soybean plots during the following two weeks yielded no additional specimens of *N. viridula*, nor were any southern green stink bugs collected in soybean during this period from weekly sampling in Wicomico County, on the eastern peninsula of Maryland (T. C. Elden, pers. comm.). Several adults and late instars of *Euschistus* spp. stink bugs were captured at the South Farm, and fifth instars and adults of the green stink bug, *Acrosternum hilare* (Say), were exceptionally common on the eastern shore of Maryland. The errant *Nezara* female was housed in the laboratory insectary (16:8 h L:D, 28°C, 65% RH) and proceeded to oviposit fertile egg masses on October 7, 13, 19, 23, 30, and November 13. Approximately half of the eggs in the sixth mass were infertile and the female died within a week of the last oviposition date.

Shortly before midnight, September 21, a hurricane with winds in excess of 215 km/h made landfall near Charleston, South Carolina, and moved rapidly to the northwest (Fig. 1 insert; Weekly Climate Bulletin No. 89/38, U.S. Department of Commerce). Though the eye of the storm (designated "Hugo") passed east of Maryland through West Virginia, this powerful hurricane encompassed the entire eastern portion of the continent after landfall (Fig. 1; Satellite Data Service Division, U.S. Department of Commerce). Thus, the most likely explanation for the appearance of *N. viridula* in Maryland is that the insect was swept northward from South Carolina by the intense counterclockwise, uplifting winds of the hurricane and deposited some 13–14 h later in Maryland. This scenario is supported by the knowledge that the insect is capable of sustained flight for at least 12 h (Kester and Smith 1984, Entomol. Exp. Appl. 35: 75–81) and, in fact, has often been collected more than 150 km from land without abnormally strong winds (ref. in Hokkanen 1986; Baust, Benton, and Aumann 1981,

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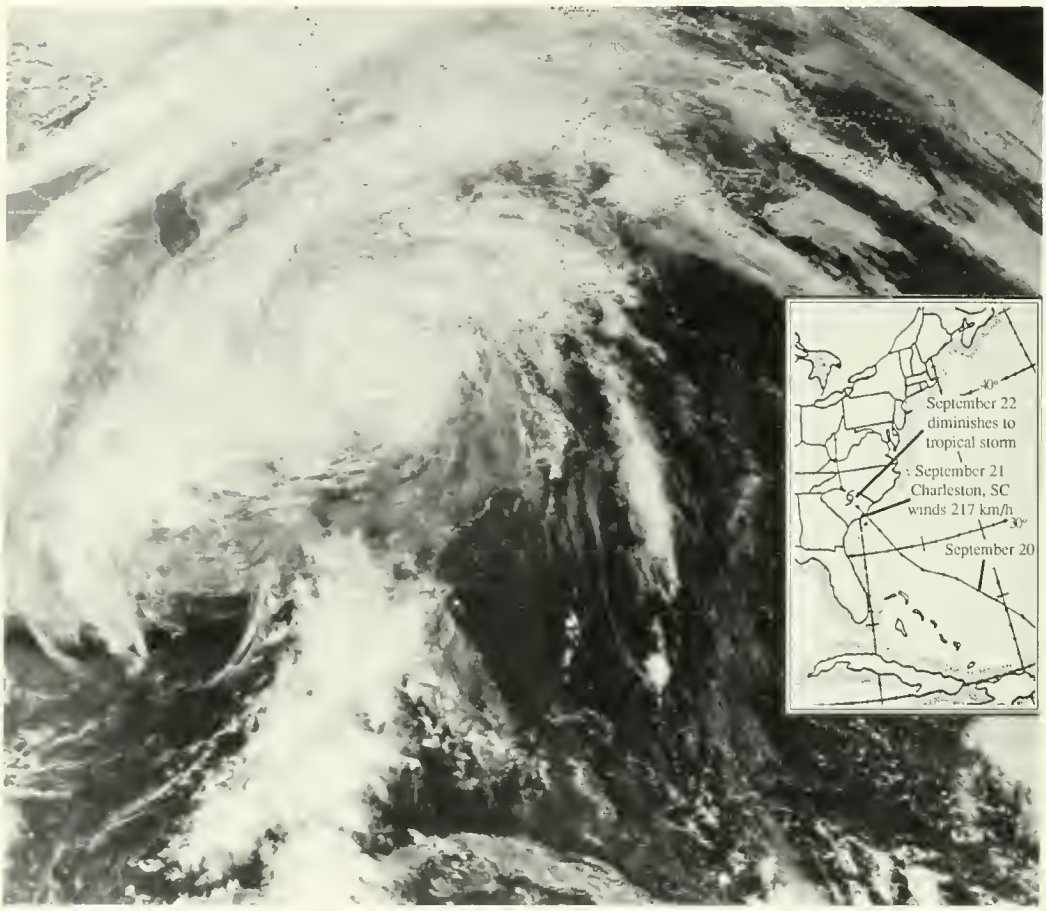

Fig. 1 Photograph: Satellite view of Hurricane Hugo at ca. 13:30, September 22, 1989. Insert: Path of Hugo the day before and after landfall.

Bull. Entomol. Soc. Am. 27: 23–25; Sparks, Jackson, Carpenter, and Muller 1986, Ann. Entomol. Soc. Am. 79: 132–139).

Dissection of five *A. hilare* females collected October 5 in Wicomico County, Maryland, revealed that these bugs were committed to diapause (large fat body with little ovarian development); a similar condition might be expected for the *Nezara* female in question had she developed in Maryland. Moreover, aeration of 18 F_1 *N. viridula* males (ca. 10 days old) produced a pheromone extract that was indistinguishable by gas chromatography from pheromone of *N. viridula* males from the southeastern U.S. (Aldrich, Lusby, Marron, Nicolaou, Hoffmann, and Wilson 1989, Naturwissenschaften 76: 173–175).

This record of a fertile *N. viridula* female about 750 km north of its probable point of origin near Charleston, South Carolina, provokes the question: Will the southern green stink bug, and other insects of similar distribution in the southeastern U.S., be encountered farther north next season than usual? In describing the long-range dispersal of certain aquatic Heteroptera via hurricanes, Herring (1958, Pan-Pac. Ent. 34: 174, 175) emphasized that "Hurricanes are not rare phenomena but occur with amazing frequency in the tropics and provide a dynamic means of distributing organisms." As

such, hurricanes should be included among Wellington's "exploitable kinds of weather" available to insects for the evolution of dispersive adaptations (1983, Bull. Entomol. Soc. Am. 29: 24–29).

I thank Dr. Owen Thompson, Department of Meteorology, University of Maryland, College Park, for helpful discussions about hurricanes and for showing me the satellite video of the landfall of hurricane Hugo. I am especially grateful to Thomas C. Elden, USDA-ARS, Germplasm Quality and Enhancement Laboratory, Beltsville, for informing me of stink bug infestations in soybean and helping to collect bugs. Tom Elden also reviewed the manuscript, as did Kent D. Elsey and Thomas J. Henry, for which I am grateful.

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A NEW SPECIES OF *STENONEMA* (EPHEMEROPTERA: HEPTAGENIIDAE) FROM NORTH CAROLINA

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Abstract.—The new species, ***Stenonema lenati*** McCafferty, is described and figured from larval specimens taken from unpolluted reaches of Piedmont rivers in North Carolina. The new species has a distinctive dorsal color pattern and is easily keyed from other *Stenonema* larvae. It apparently belongs to Cluster IIIB of the subgenus *Maccaffertium* and is perhaps most closely related to *Stenonema mexicanum*. It and some other *Stenonema* species demonstrate highly restricted geographic and ecological distributions.

Key Words: mayflies, Heptageniidae, *Stenonema*, new species

Stenonema larvae that were taken in larger rivers of the North Carolina inner coastal plain but that could not be definitively identified to any known species using Bednarik and McCafferty (1979) were first found and brought to my attention in 1985. Subsequent examination of this material revealed that these populations represent a new species of *Stenonema*, the second of which to have been discovered since the extensive revision of the genus by Bednarik and McCafferty (1979). Its discovery, much like that of *Stenonema bednariki* McCafferty in Kentucky and Missouri (McCafferty 1981), was precipitated by aquatic biologists conducting water quality studies and then being able to recognize enigmatic populations through the use of comprehensive taxonomic literature.

The new species is based on the larval stage alone since adults have yet to be reared. The species-level morphological characters in *Stenonema*, however, are primarily and sometimes entirely based on the larval stage. Whereas larvae tend to have specific characterization, perhaps related to adaptations to specific running water habitats and ecology, adults have been less prone to morphological evolution, possibly due to the relatively young geological age of the group as hypothesized by Bednarik and McCafferty (1979). The new species belongs to the subgenus *Maccaffertium*. I name it in honor of David Lenat in recognition of his collecting of the new material.

Stenonema lenati McCafferty

New Species

Fig. 1

Larva (in alcohol).—Mature length excluding caudal filaments: 11.0 mm (male) to 14.0 (female).

Head: Vertex (Fig. 1) generally medium to dark brown with fine, pale speckling and with small pale area anterior to median ocellus, pair of pale areas extending between compound eyes and lateral ocelli, large pale areas anterolateral and lateral to compound eyes, and 3 pale areas along posterior margin between compound eyes, sometimes becoming continuous; narrow brown band sometimes extending laterad of each compound eye, dividing anterolateral pale areas from lateral pale areas; lateral and posterior

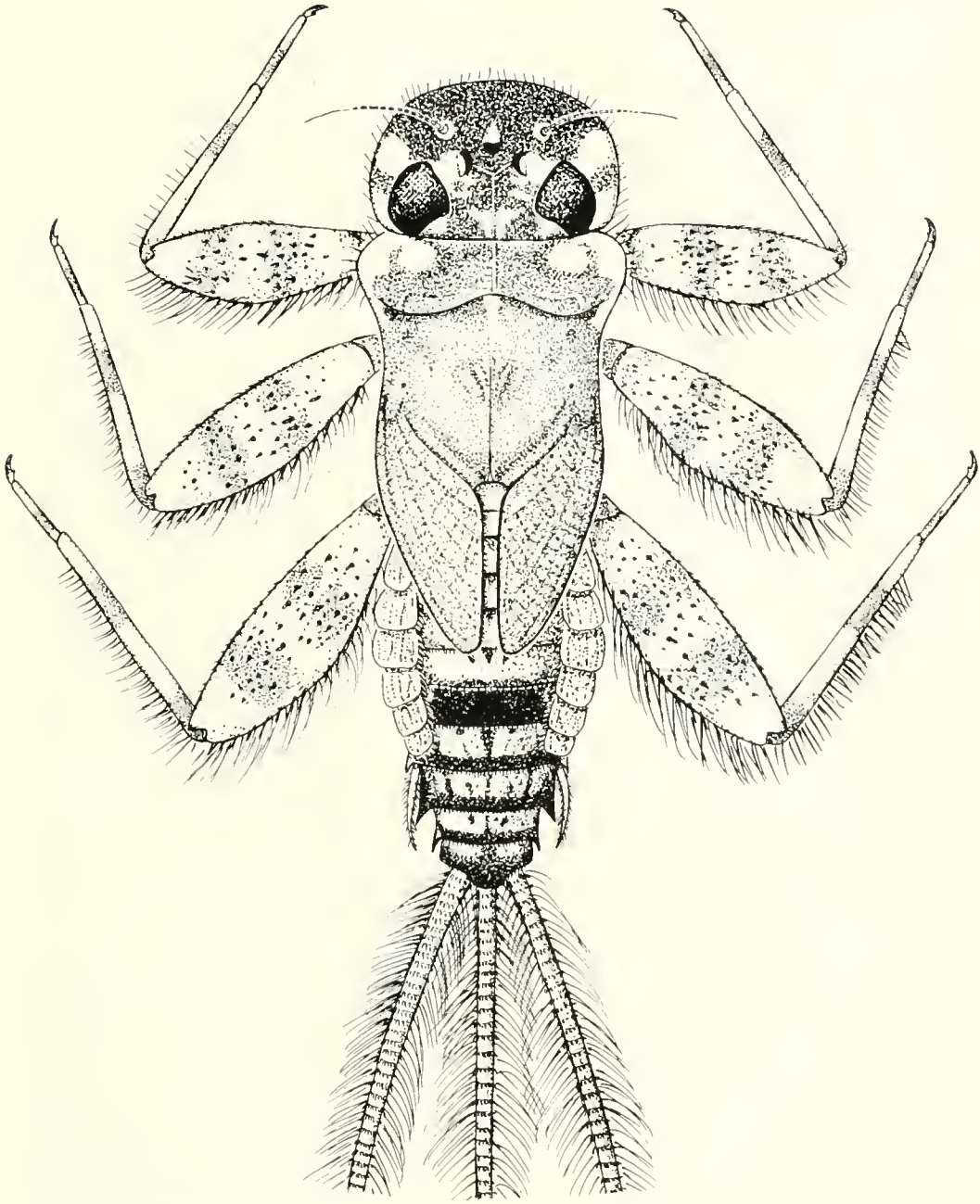

Fig. 1. *Stenonema lenati*, larva.

pale areas obliterated to large degree in mature males by well-developed compound eyes. Scapes of antennae light; pedicels and bases of flagella dark brown; remainder of flagella light. Mandibles each with 8–10 teeth on inner margin of outer incisor. Maxillae each with 1–3 spinelike setae on crown of galealaciniae (usually 2, with pectination

poorly developed on subapical spinelike seta and hardly developed on terminal seta), and with 25–35 hairlike setae on galealacinial crown, and 19–26 setae in submedial row of galealaciniae.

Thorax: Nota (Fig. 1) generally medium brown; pronotum with pale lateral and anterolateral marginal areas and pair of distinctive sublateral, pale spots at anterior margin. Legs (Fig. 1) generally pale with brown banding dorsally; all tarsi with single, brown band at midlength; fore- and midtibiae with single, broad bands at approximately midlength, most prominent on foretibiae; hindtibiae without bands; all femora with pair of broad bands, sometimes appearing diffuse or coalescing with each other, more basal bands of mid- and hindfemora often broken and appearing more as 2 large markings. Dorsal armature of forefemora consisting of small, mostly blunt, spinelike setae scattered over apical ½ to ¾ of surface; posterior margin of forefemora with short, spinelike setae and long, hairlike setae; anterior margin without distinct rows of either spinelike or hairlike setae. Foretarsal claws adenticulate. Hindfemora not conspicuously broader than fore- and midfemora.

Abdomen: Dorsally (Fig. 1) pale with conspicuous dark brown and light brown patterns: terga 1–5 with variable markings but often with triangulate anteromedial mark, pair of submedian small spots, and some sublateral markings, sometimes diffuse. Some individuals, however, with terga 1 and 2 generally light; tergum 3 almost completely dark; tergum 4 with large, dark, sublateral markings; and tergum 5 with pair of small, dark, submedian spots and posterior, dark brown transverse band. Terga 6–10 more consistently patterned among individuals, varying mostly in degree and extent of pigmentation: terga 6 almost entirely brown to dark brown; terga 7–9 with conspicuous, dark, transverse bands at posterior margin, often dark, medial, longitudinal stripe with shape somewhat variable, darkened lateral areas under gills, and pair of small, submedian spots; tergum 10 with dark pigmentation covering anywhere from posterior half to virtually entire tergum. Rows of well-developed spinules along posterior borders of all terga. Lateral patches of light, hairlike setae well developed on terga 3–7. Ventrally, sterna 1–6 pale, without markings; sterna 7 and 8 entirely pale with no markings to somewhat ferruginous with small, dark, anteromedial, triangulate markings (anterior markings usually seen beneath overlapping edge of preceding sternum) and narrow, diffuse shadings or markings; sternum 9 of females ranging from pale to ferruginous with markings ranging from having no anterolateral markings and pair of sublateral, dark spots at posterior margin to having anterolateral markings and well-developed dark band following rather horseshoe shaped distal margin, darkest at sublateral areas corresponding to spotted areas of lighter individuals; sternum 9 of males instead usually with pair of diffuse to well-defined spots sublaterally and subterminally and diffuse, subterminal, transverse band (tips of developing genital forceps also shaded with ferruginous in mature individuals). Posterolateral projections not developed on segments 1–5; projections on segment 8 slightly larger than those of segment 7 and much larger than those of segment 10. Gills 1–6 truncate apically; gills 7 untracheated. Caudal filaments uniformly ferruginous, with short, spinelike setae and long, hairlike setae well developed on each segment.

Holotype.—Mature male larva, North Carolina: Stanley Co.: Rocky River at Norwood, March, 1985, D. R. Lenat, deposited in the Purdue Entomological Research Collection (PERC), West Lafayette, IN.

Paratypes.—Five mature female and four mature male larvae (some mouthparts slidemounted), same data as holotype, all in PERC except one mature male larva at United State National Museum, Washington, D.C.

Additional material examined.—Ten larvae, North Carolina: Chatham Co., Haw River, May, 1985, D. R. Lenat, in PERC; nine larvae, North Carolina: Moore/Randolph Cos., Deep River, August, 1985, D. R. Lenat, in PERC.

Discussion.—The dorsal color pattern of abdominal segments 6–10 (Fig. 1) found in *S. lenati* is unlike that of any other *Stenonema*. Many species have a darkened tergum 6, e.g. *S. pulchellum, S. mexicanum,* and *S. exiguum*; however, their following terga differ considerably from those of *S. lenati*. The pattern of sternum 9 of either males or females are also distinctive but are subject to considerable individual variability. Sternum 9 of *S. femoratum* may have a darkened, horseshoe-shaped, posterior margin similar to that of the female larva of *S. lenati*, but the remainder of the ventral abdominal pattern is very different. The pattern of the vertex and pronotum together can also be used to diagnose this species, particularly when taken in combination with other characters.

By using the larval key of Bednarik and McCafferty (1979) and ignoring the color patterns mentioned above, one would tend to key *S. lenati* to couplet 18 and *S. integrum* [= *S. mexicanum* (see McCafferty 1984)]. This is due to the large number of hairlike setae but only one or two spinelike setae found on the crown of the galealacinia. Couplet 18 should be modified into a triplet as follows to accommodate identification of *S. lenati*:

18. Abdominal terga 7, 8, and 9 together with a distinct V-shaped pale area; galealacinial crown with 2–3 spinelike setae . . *S. mexicanum*
– Abdominal terga 7, 8, and 9 each pale with darkened lateral areas, posterior borders, variable median stripe, and pair of submedian, small spots; galealacinial crown with 1–3 spinelike setae (usually 2 and with only 1 conspicuously pectinate) . . . . . *S. lenati*
– Abdominal terga 7, 8, and 9 with various patterns but not exactly as either of above patterns; galealacinial crown with 3–7 spinelike setae (if only 3, then terga 8 and 9 mostly dark) 19

It is difficult to determine the exact relationships of *S. lenati*. It is definitely a member of the subgenus *Maccaffertium*, sharing truncated gills 1–6 and untracheated gills 7 with other members of that subgenus. The new species probably belongs to species Cluster III (Bednarik and McCafferty 1979) because of the loss of posterolateral projections on anterior segments of the larval abdomen. This proposition, however, is contingent on male adult penes and eye separation characters proving to be consistent with others in this phyletic position. This appears likely because, based on its larval characteristics, the species would furthermore belong to Cluster IIIB, a group which retains considerable hairlike setae on the galealacinial crown. Cluster IIIB also includes *S. modestum, S. smithae,* and *S. mexicanum*.

The reduction of spinelike setae on the galealacinial crown of *S. mexicanum* and *S. lenati* suggests a possible sister relationship of these two species. Based on published distributions, the geographically restricted *S. lenati* apparently does not overlap with the relatively very widespread *S. mexicanum* (see Bednarik and McCafferty 1979 under *S. integrum*). This suspected allopatry is supported by collecting records of D. R. Lenat (pers. comm.), who has not collected the two species together in North Carolina. *Stenonema lenati* has been taken only in coastal plains, whereas records of *S. mexicanum* in North Carolina are from other regions of the state.

Stenonema lenati larvae appear to be limited to unpolluted sections of Piedmont rivers near the fall line. They have been found in slower currents and have been taken cohabiting with the following other heptageniid mayflies: *Stenonema exiguum, S. femoratum* (rarely), *S. modestum, S. terminatum, Stenacron interpunctatum, S. pallidum, Heptagenia marginalis,* and *Leucrocuta aphrodite*.

With the discovery of *S. lenati*, there are now four species of *Stenonema* known to

have highly restricted distributions and what appear to be highly restricted ecological requirements. The other three are *S. bednariki, S. carlsoni,* and *S. sinclairi.* All of these are clean-water species (Lewis 1974, 1979, McCafferty 1981) and may be in jeopardy of survival because of narrow ecological tolerances. Of the four, only *S. lenati* is found in large rivers, the others occurring in smaller streams.

Collections of *S. lenati* larvae were made in March, May, and August. Only the March collections included mature individuals with darkened wingpads. May and August samples contained predominantly middle instar larvae and no mature individuals. While such data suggest an early spring emergence and possibly suggest another mid-summer emergence, data are too limited to draw definite conclusions about voltinism and other aspects of phenology at this time.

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DESCRIPTIONS OF THE LARVA AND PUPA OF *FLAVOHELODES THORACICA* (GUÉRIN-MÉNEVILLE) WITH NOTES ON APHYTOTELMA ASSOCIATION (COLEOPTERA: SCIRTIDAE)

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Abstract.—Descriptions of the larva and pupa of *Flavohelodes thoracica* (Guérin-Méneville) are given and based on specimens collected and reared from a phytotelma (water-filled treehole) in a *Quercus* sp. These descriptions are presented in order to facilitate the recognition of immature *F. thoracica* and to document the occurrence of this species in phytotelmata. Morphological comparisons are made with *F. flavicollis* (Kiesenwetter). The status of phytotelmata as a habitat association with the genus is briefly discussed.

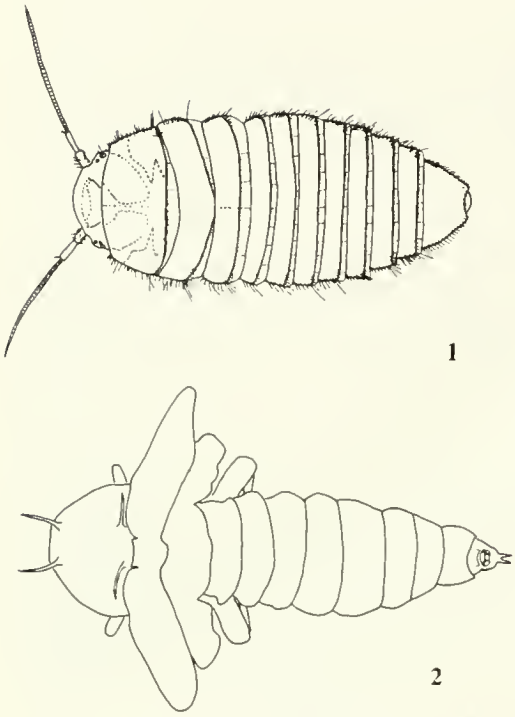
Key Words: immature stages, phytotelmata, Scirtidae, *Flavohelodes*

Scirtidae larvae inhabit a wide variety of restricted lentic habitats including phytotelmata (e.g. water-filled treeholes, tank-forming Bromeliaceae); shallow, leafy groundpools; and leaf packs in nearly still waters of stream sidepools. Larvae are relatively easily collected from these habitats, occasionally in large numbers. In spite of this and the relative ease of rearing, life stages or species/habitat associations have been published for few species of Scirtidae. Among those treated in detail are *Prionocyphon discoideus* Say (Osten-Sacken 1862, Snow 1958a, b), *P. serricornis* Müller (Benick 1924, Rohnert 1951, Horion 1955, Kitching 1969, 1971, 1983), *P. niger* Kitching and Allsopp (1987), *Scirtes championi* Picado (1913), and *Flavohelodes flavicollis* (Kiesenwetter) (Klausnitzer 1980).

Klausnitzer (1974) recognized the *Elodes flavicollis* species group as distinct from the remaining species of the genus. Later, he (Klausnitzer 1980) elevated this species group to generic status, naming it *Flavohelodes*. This action was partially based on larval mouthpart and antennal modifications which he interpreted as adaptations to phytotelmata. Klausnitzer (1980) also reported the larval stages of *F. flavicollis* (Kiesenwetter) as having been recently discovered inhabiting water-filled treeholes in Europe. This represents the sole source of published microhabitat data for the genus until now. In this paper, we add another with the description of the larval and pupal stages of *Flavohelodes thoracica* (Guérin-Méneville) which were collected and reared from a *Quercus* phytotelma near Great Falls, Montgomery Co., Maryland.

METHODS

Collection and rearing.—Loose leaves and the leaf pack at the bottom of the treehole were removed by hand and long forceps and sorted in a white porcelain pan. Some larvae were immediately placed into vials contain-

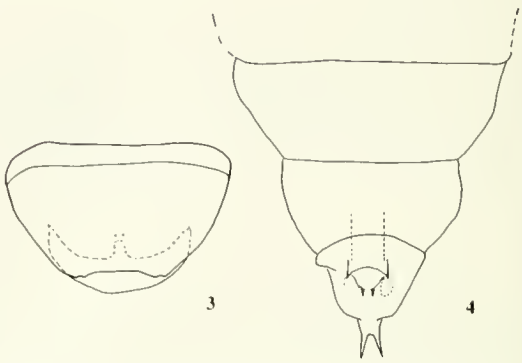


Figs. 1, 2. *Flavohelodes thoracica* (Guérin-Méneville), 1. larva, dorsal habitus, dotted lines on pronotum indicate patterns of melanization, the median, longitudinal vitta and the anterolateral arms being lighter; 2. pupa, dorsal habitus.

ing 70% ethanol for preservation. The remainder were segregated into plastic containers with leaf litter and water from the phytotelma, and returned to the lab. Water was removed by siphoning with rubber laboratory tubing or commercial basting syringe.

Larvae to be reared were placed into 4–6 dram glass, stoppered vials. Each vial was partially filled with treehole water and a few leaf fragments from the original treehole. Personal observations have demonstrated that mature larvae crawl out of the water to pupate, attaching the abdominal apex to the leaf surface. Since attachment to the glass walls of a vial has not been observed, it may be essential to orient the leaf fragments so that portions of them protrude well above the level of the water.

Dissections and illustrations.—Dissections were performed in 70% ethanol. Dissected structures were cleared in an aqueous KOH solution, rinsed in distilled water, and observed in glycerine. The dissected structures were stored in genitalic microvials with a drop of glycerine; these microvials were than placed in glass alcohol vials along with the remainder of the specimen.



Figs. 3, 4. *Flavohelodes thoracica* (Guérin-Méneville), 3. larva, abdominal terga 8–9, dorsal view; 4. pupa, apical abdominal segments, dorsal view.

Habitus illustrations were drawn with the aid of a camera lucida attached to a Wild M5A dissecting microscope. Mouthpart illustrations were prepared using a microprojector. Actual preparation of dissections for illustration were with the K-Y procedure as described by Young and Stribling (1990).

In the following description, terms for mouthpart and abdominal characters of the larva were translated directly from or modified after Hannappel and Paulus (1987). Some terms in the pupal description were adopted from Rozen (1963).

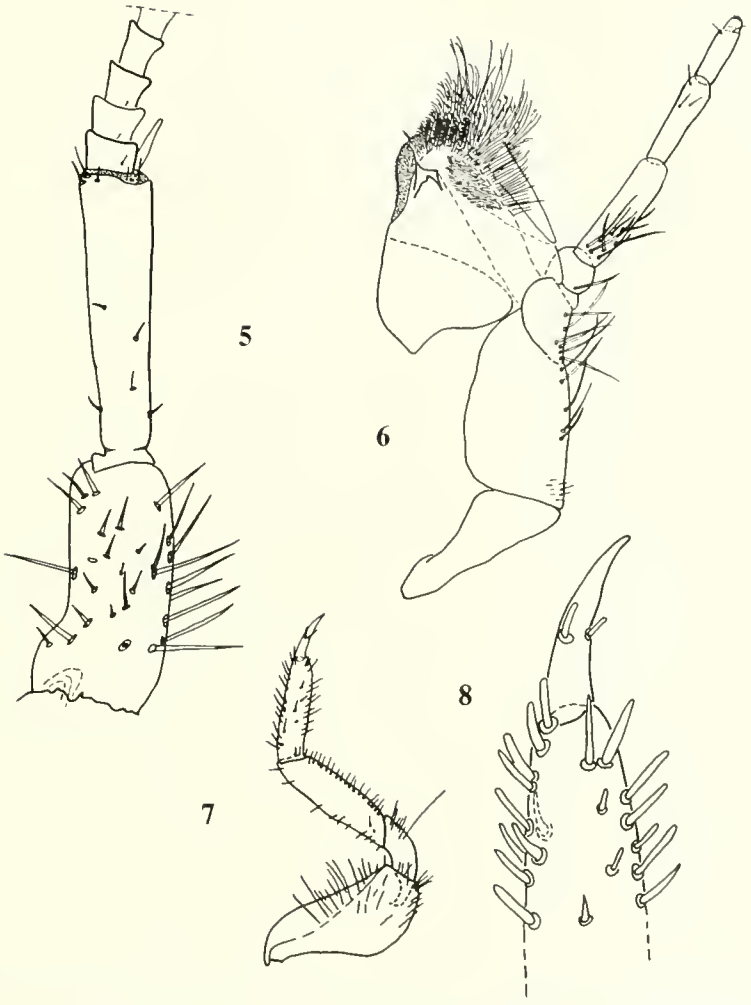
Voucher specimens are deposited in the personal collections of the authors (DYCC, Madison, Wisconsin and JBSC, Woodbridge, Virginia).

Flavohelodes thoracica (Guérin-Méneville)

Description.—Mature larva (Figs. 1, 3, 5–12).

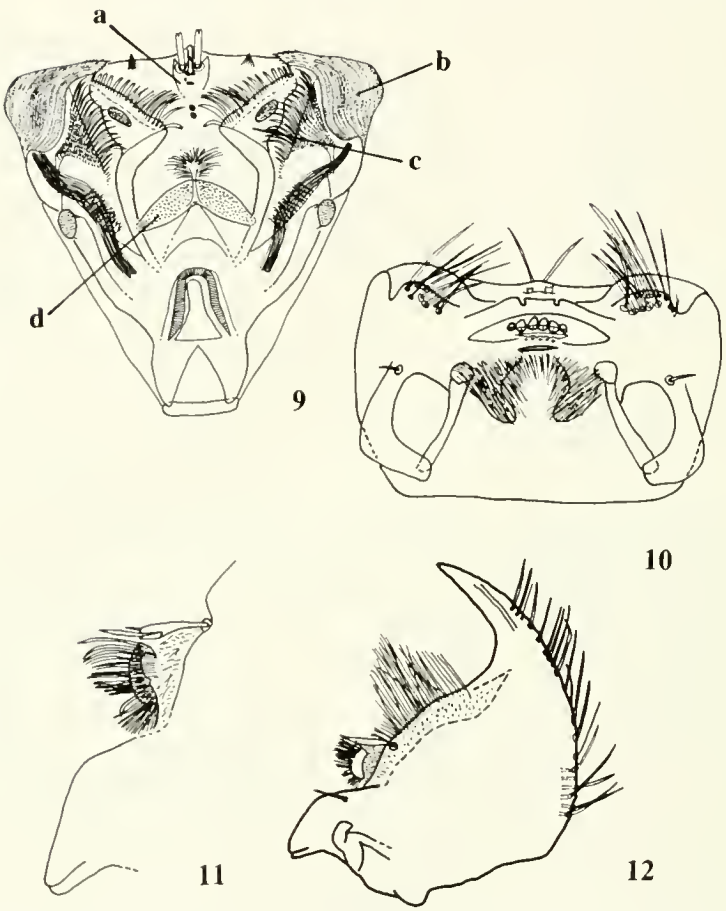
Body size.—Length 6–10 mm, most specimens 7–9 mm; maximum width (usually in thoracic area) 1–2 mm.

Head.—Antennal scape ca. $\frac{4}{5}$ length ped-



Figs. 5–8. *Flavohelodes thoracica* (Guérin-Méneville), larva, 5. basal antennal segments, dorsal view; 6. left maxilla, ventral view; 7. metathoracic leg; 8. mesothoracic tarsus and tarsungulus.

icel (Fig. 5), 37–43 flagellomeres (Fig. 1), scape with larger and approx. 2× as many setae on medial surface as on lateral aspect; pedicel with 10–12 small, unevenly scattered setae, apically with 4–6 small setae, and a single, very large, stout seta mesally on apex (Fig. 5); 3 non-melanized stemmata either side of cranium in a dorsal, anterior-posterior row; anterior stemma separated from posterior pair by melanized band; row of large subocular setae; clypeolabrum (epipharynx) (Fig. 10) with ventral lobes not protruding anteriorly past margin of clypeolabral forewall, 6 teeth anterad of 5 subdental sensilla; mandibular prostheca (Figs. 11, 12) of 2 main sections, proximal sclerite with row of setae, and large, distal compound macroseta with main body socketed to the mandible and 2–3 distal subdivisions; mola cleft proximally; maxilla (Fig. 6) with 3 palpomeres, 5 galeal comb setae visible in ventral view; lacinial setal area of short, dense pile of mesally directed setae; hypopharynx (Fig. 9) with two apically notched hypopharyngeal teeth, setigerous sclerite (Fig. 9a) with two long setae and four cam-



Figs. 9–12. *Flavohelodes thoracica* (Guérin-Méneville), larva, 9. hypopharynx, dorsal view; a—setigerous sclerite, b—grip apparatus, c—comb plate, d—central compress; 10. clypeolabrum (epipharynx), ventral view; 11. left mandible, mola, and prostheca, ventral view; 12. left mandible, ventral view.

paniform sensilla, usually arranged in row (specimen figured has one lateral sensillum apically offset); one pair of medial campaniform sensilla proximad to setigerous sclerite; comb plate (Fig. 9c) with oval setal patch bearing 18–20 teeth; grip apparatus (Fig. 9b) covered anterolaterally with short, fine setae, posteriorly covered with thicker, more distinct setae (much longer on mesal margin); setal cluster near the anterior margin between setigerous sclerite and grip apparatus; central compress (Fig. 9d) wing-shaped, completely covered with tiny tubercles; labium broad, each palpus of 2 palpomeres.

Thorax (Fig. 1).—Mediodorsal length ratio (pro- : meso : metathoracic nota) 2:1:1; paler bands of melanization extend from anterolateral pronotal angles to midpoint of posterior pronotal margin, meso- and metathoracic nota somewhat paler at middorsal line; notal setation sparse except at margins, setae usually of increasing length from anterior to posterior angles; nota punctate, punctations evenly distributed, each with single, short fine seta; prothoracic legs (Figs. 7, 8) slightly shorter than meso- and metathoracic legs, other features invariant; coxae (Fig. 7) transverse (some appear conical if larva has inflated in preservation), sparsely setose, most setae dispersed on ventral and anterior surfaces; femur with two longitudinal, parallel rows of strong setae on outer

surface, continuing around tibial insertion; tibia with stout setae on lateral and mesal surfaces, setation sparse anteriorly and posteriorly; tarsungulus (Fig. 8) with two strong, subapical setae; meso- and metathoracic sterna with intercoxal patches of long setae.

Abdomen (Fig. 1).—Eight visible segments, gradually decreasing in circumference and increasing in mediodorsal length posteriorly; punctation and setation similar to thoracic nota; tergum eight (Fig. 3) emarginate and slightly concave apically, ninth tergum as in Fig. 3.

Pupa (Figs. 2, 4).—Body length 5.5 mm; head smooth; dorsally covered with short, fine setae concolorous with cuticle; pronotum with two anterior and two posterior spines ("tubercles" of Rozen [1963]); elytra long, approx. ⅓ body length, projecting postero-laterally; nine abdominal segments, segment nine with short, bifurcate, terminal projection, ninth tergum (Fig. 4) with blind posterior pit, bounded dorsally by sclerite with 2 acute, lateral apices, and ventrally with 2 small spines.

Material examined (and repositories): MARYLAND, Montg. Co., near Great Falls, 02 June 1987, J. B. Stribling & W. E. Steiner/reared from larva in water from tree hole (14 larvae, 2 exuviae, 1 pupa, 3 adults; DYCC); (same data)/in water from tree hole (13 larvae; 7 DYCC, 6 JBSC).

Comparisons with *Flavohelodes flavicollis* (Kiesenwetter)

Comparisons of *F. thoracica* are based on descriptions in Hannappel and Paulus (1987). Some structures are unavailable for comparison because they have not been described in prior publications and the lack of specimens of *F. flavicollis*. Those which are common to our studies are discussed here.

Hypopharynx (Fig. 9).—Near the anterior margin between the grip apparatus and the setigerous sclerite there exists a cluster of setae which is lacking in *F. flavicollis*. A further difference is the existence of a row of heavier spines or setae on the anterior surface of the grip apparatus in *F. flavicollis* that is lacking in *F. thoracica*.

Clypeolabrum (Fig. 10).—In *F. flavicollis*, the ventral lobes are protruding past the anterior margin, there are 6 subdental sensilla, the setation of the anterior lobes is more uniform and stouter, the pair of medioanterior setae is short, and the lateral setation is abundant. In contrast, in *F. thoracica*, the ventral lobes do not protrude past the anterior margin, there are 5 subdental sensilla, the setation of the anterior lobe is less uniform and less stout, the pair of medioanterior setae is longer, and lateral setation is lacking.

Mandible (Figs. 11, 12).—The main species differences exist in the form of the prostheca. In *F. flavicollis* this structure is not setose and does not have an associated compound macroseta as is found in *F. thoracica*.

Maxillary palpus (Fig. 6).—Setal abundance and distribution are similar in the two species. In palpomere 1 of *F. thoracica* setation is more proximal than that of *F. flavicollis* which is more evenly and longitudinally distributed.

Status of the *Flavohelodes*/phytotelmata association

In his paper elevating the *flavicollis* species group to generic status, Klausnitzer (1980) hypothesized phytotelmata use as an ecological synapomorphy. Here, we have documented hardwood phytotelmata as a habitat for larval development of *F. thoracica* in support of this hypothesis. Although this study confirms phytotelmata use, we still know little of the degree of habitat specificity for this species. For example, are phytotelmata necessary for *F. thoracica* development or is it only one of the many potential breeding sites?

Frank and O'Meara (1985) found habitat segregation by oviposition site preference in bromeliad-breeding *Wyeomyia* spp. (Diptera: Culicidae) and attributed this to both microhabitat and macrohabitat differences. Preference of *Tillandsia utriculata* Linnaeus over *Catopsis berteroniana* (Schultes) Mez

ex de Candolle (Bromeliaceae) phytotelmata for oviposition was interpreted as a microhabitat difference. In another experiment reported in the same paper, bromeliads in shaded habitat were found to be preferred for oviposition over those in non-shaded locations. The shaded vs. non-shaded habitats were interpreted as macrohabitat differences.

In order to categorize our *F. thoracica*–phytotelma association as microhabitat or macrohabitat, in the sense of Frank and O'Meara (1985), as well as further testing of Klausnitzer's (1980) hypothesis, more must be known about the ecological distribution of this species. Further collection and rearing of scirtid larvae from hardwood phytotelmata and other potential breeding sites, with documentation of habitat specifics, will allow these questions to be answered.

Acknowledgment

We are grateful to W. E. Steiner (Department of Entomology, Smithsonian Institution, Washington, D.C.) for accompaniment in the field and for his suggestions; to P. J. Spangler (Entomology, Smithsonian Institution) and D. R. Whitehead (USDA—Systematic Entomology Laboratory, Washington, D.C.) for providing space and equipment; and, to M. Rodón-Naviera, P. Thaler, and E. Barrows (Georgetown University) for comments and suggestions on earlier drafts of the manuscript. We thank several anonymous reviewers for well-taken suggestions.

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NOTE

Andrena macra Mitchell (Hymenoptera: Andrenidae) Overwinter and Delay Spring Emergence in Virginia

Andrena macra Mitchell are known from West Virginia and Maryland southward to Florida, and westward to Texas and Oklahoma (LaBerge 1985. Trans. Amer. Entomol. Soc. 112(3): 191–248). The only biological investigation of this species was done by Sivik (1954. Entomol. News 65(10): 253–256), where he witnessed the emergence of adults, and determined the distribution of nests in a site near East Raleigh, North Carolina. The purpose of this note is to present some unusual observations on the life cycle of this solitary, soil-nesting bee.

The nesting site observed in this study was adjacent to a graveled off-road on the United States Marine Corps Reservation in Quantico, Virginia. *Andrena macra* nests were excavated so that the overwintering brood of this bee could be observed. Excavations were conducted on the following days of each month: 15, 17, 19, 31 March 1984; 7, 12, 26 April 1984; and 2, 10, 11 May 1984. Brood were removed from the nests with a microspatula and placed, individually, inside 4-dram glass shell vials. The numbers of live *A. macra* found on daily excavations beneath the surface of this site during Winter and Spring 1984 are listed in Table 1. A total of 59 overwintering prepupae were kept in the laboratory at room temperature (24–27 degrees Celsius), inside the shell vials, to see if and when they would complete their development to the mature adult stage. Eleven were reared successfully (Table 2). Prepupae required 78 ± 8.4 days (mean and standard error) to metamorphose into pupae. These pupae required 21 ± 1.3 days to metamorphose into mature adults.

Andrena macra overwintered in the prepupal and adult stages of development. Species of *Andrena* were previously known to overwinter only as adults (Linsley 1958. Hilgardia 27(19): 543–599). Some of the overwintering *A. macra* also delayed spring emergence in 1984. The evidence in favor of delayed emergence is as follows: (1) prepupae were found inside nest brood cells on the same days that adults had emerged and were present on the surface of the nesting site, and (2) prepupae that were found in March and May completed their development to the mature adult stage near the end, or after the end, of the Spring 1984 nesting season (see Table 2). All adult nesting activities had ceased by mid-June 1984.

Delayed emergence has been reported for several species of *Andrena* distributed in the western United States. *Andrena mojavensis* Linsley and MacSwain and *Andrena ominigra clarkiae* Linsley and MacSwain delayed spring emergence in California and these spring seasons were unfavorable for host flower blooming (Linsley et al. 1964. Univ. Calif. Publ. Entomol. 33(2): 59–98; MacSwain et al. 1973. Univ. Calif. Publ. Entomol. 70: 1–80). Thorp (1979. Ann. Mo. Bot. Gard. 66: 788–812) indicated that a species of *Andrena* delayed emergence dur-

Table 1. The numbers of live *Andrena macra* found in nest brood cells during daily excavations in 1984.

Prepupae	Adults	Date Found
28	15	15 March
8	2	17 March
2	24	19 March
7	—	31 March
1	—	7 April
—	2	12 April
10	4	26 April
8	2	2 May
5	—	10 May
3	1	11 May

Table 2. Results of the rearing experiment in 1984.

Date Found	*P-P	Date at Mature Adult Stage	Sex of Reared *Andrena macra*
15 March	40	4 June	F
15 March	49	6 June	M
15 March	51	13 June	M
15 March	51	18 June	M
15 March	70	8 July	M
15 March	83	15 July	M
15 March	83	17 July	F
31 March	126	30 August	F
2 May	95	27 August	M
2 May	98	29 August	M
10 May	109	23 September	F

* P-P = number of days required for prepupae to metamorphose into pupae.
F = female; M = male.

ing the time that a drought occurred in California.

Delaying spring emergence in the eastern United States may insure survival for *A. macra* especially when they nest in dense aggregations. Female *A. macra* of large nesting sites may have to rely on limited sources of pollen and nectar to provision their nest brood cells with, each spring season. Emergence of the individuals of a population in two years, instead of one, will prevent the depletion of floral resources.

Dr. W. E. LaBerge (Illinois Natural History Survey) identified the *A. macra*. This research was a portion of a M.S. thesis submitted to the graduate faculty (Department of Zoology) at Howard University. Partial support was made available by a Minority Biomedical Research grant (RR-08016) awarded to Drs. R. M. Duffield and J. Wheeler from the Division of Research Resources, National Institutes of Health.

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EFFECT OF ANTIOXIDANTS ON EASTERN SUBTERRANEAN TERMITE (ISOPTERA: RHINOTERMITIDAE) ORIENTATION TO FUNGAL EXTRACT

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Abstract.—Dichloromethane and cyclohexane extracts of wood decayed by *Gloeophyllum trabeum* induce trail-following, arrestment, and/or aggregation of *Reticulitermes flavipes* in behavioral bioassays. In trail-following assays with *R. flavipes* workers, addition of the antioxidant BHA completely suppressed termite response to the fungal extracts. Addition of the antioxidant BHT did not eliminate termite responses to the extracts, but concentration-dependent repellency was noted in orientation (preference) assays with individual termites and groups of workers. As measured by *R. flavipes* behavioral response, addition of BHT at the concentrations tested did not increase the longevity of the active semiochemicals in *G. trabeum* extracts.

Key Words: *Reticulitermes*, termite behavior, *Gloeophyllum*, decay fungus, semiochemicals

Wood decayed by the fungus *Gloeophyllum trabeum* (Pers. ex Fr.) Murr. (Basidiomycetes: Polyporaceae) contains the compound (*Z,Z,E*)-3,6,8-dodecatrien-1-ol (Matsumura et al. 1969) and other unidentified chemicals (Watanabe and Casida 1963, Ritter and Coenen-Saraber 1969) that affect the orientation behavior of subterranean termites (Isoptera: Rhinotermitidae). Solvent extracts of wood decayed by *G. trabeum* and other decay fungi (Grace and Wilcox 1988) elicit both trail-following and aggregation in *Reticulitermes* species (Esenther et al. 1961, Allen et al. 1964, Grace 1989b).

Currently, subterranean termites are excluded from buildings by the injection of large quantities of insecticides into the surrounding soil. An alternative approach is the development of toxic baits employing decayed wood to contaminate foraging termites and eradicate the colony through trophallaxis and grooming behavior (Esenther and Beal 1979). Natural or synthetic chemical termite "attractants" would offer more flexibility than decayed wood in developing such baits, and toxic analogues of dodecatrienol have been investigated by Carvalho and Prestwich (1984). In addition, subterranean termites are able to follow a chemical gradient (Clement et al. 1988, Grace et al. 1988), and compounds aggregating foragers might prove useful in enhancing the efficacy of pesticides applied to the soil for termite control.

The study reported here was undertaken to determine whether addition of the antioxidants BHA and BHT to solvent extracts of wood decayed by *G. trabeum* could increase the longevity of the compounds inducting a positive orientation response in the eastern subterranean termite, *Reticulitermes flavipes* (Kollar). These antioxidants

Table 1. Mean (±SE) distance traveled by *Reticulitermes flavipes* workers on artificial trails drawn with solvent (controls) and with dichloromethane extracts of *Gloeophyllum trabeum* decayed red pine containing the antioxidants BHT and BHA. Trails were air-dried 15 minutes, and each mean represents 25 individual assays. Means followed by the same letter are not significantly different at the 0.05 level (ANOVA, REGW multiple F test).

Treatment	Mean Distance (mm)
G. trabeum	35 ± 8b
G. t. + BHT (1 mg/ml)	48 ± 9ab
G. t. + BHT (10 mg/ml)	66 ± 12a
G. t. + BHA (1 mg/ml)	2 ± 1c
G. t. + BHA (10 mg/ml)	1 ± 1c
Dichloromethane Control	3 ± 1c
D.C. + BHT (1 mg/ml)	0 ± 0c
D.C. + BHT (10 mg/ml)	2 ± 1c
D.C. + BHA (1 mg/ml)	1 ± 1c
D.C. + BHA (10 mg/ml)	4 ± 3c

have been found to protect some semiochemicals with internal conjugated dienes from both oxidation and isomerization (Ideses and Shani 1988, Shani and Klug 1980) and thereby enhance their field life in pest management applications.

Methods

Termites.—Foraging eastern subterranean termites, *R. flavipes*, were collected from corrugated paper rolled within short lengths of plastic pipe buried just below the soil surface at a site in the city of Scarborough, Ontario (Grace 1989a). Prior to their use in bioassays, termites were maintained on corrugated paper and filter paper in plastic boxes in an unlighted incubator (27 ± 0.5°C, 90 ± 5% RH).

Fungus extracts.—Red pine, *Pinus resinosa* Ait., decayed for 6–8 weeks after inoculation with *G. trabeum* was provided by E. E. Doyle and K. Seifert, Forintek Canada Corp., Ottawa, Ontario. Ten grams of decayed wood, ground in a Wiley mill to pass a 40-mesh screen, were shaken in 100 ml dichloromethane or cyclohexane for 15 minutes at room temperature (24°C), and gravity-filtered through Whatman No. 1 filter paper to yield approximately 70 ml of filtrate. The antioxidants 3(2)-*tert*-butyl-4-hydroxyanoisole (BHA) and 2,6-di-*tert*-butyl-4-methylphenol (butylated hydroxytoluene, BHT) were purchased from Sigma Chemical Co., St. Louis, MO.

Trail-following assay.—Three bioassays were used to test the effects of *G. trabeum* extracts containing either 1, 10, or 100 mg/ml BHA or BHT on *R. flavipes* orientation behavior. In the trail-following assay, described by Grace and Wilcox (1988), a straight 20-cm line was drawn on tracing paper with 4 μl of solution, applied by a microliter syringe. This artificial trail was

Table 2. Mean (±SE) distance traveled by *Reticulitermes flavipes* workers on artificial trails drawn with dichloromethane and cyclohexane extracts of *Gloeophyllum trabeum* decayed red pine containing BHT. Trails were air-dried for different time intervals, and each mean represents 25 individual assays. Treatment means with the same solvent in each column followed by the same letter are not significantly different at the 0.05 level (*t* test, or ANOVA and REGW multiple F test).

Solvent	Treatment	Trail Aeration Time (minutes)						
		15	45	60	75	105	120	135
CH_2Cl_2	*G. trabeum*	47 ± 11a	30 ± 6a		17 ± 5a	15 ± 5a		10 ± 3a
	G. t. + BHT (1 mg/ml)	45 ± 10a	30 ± 8a		23 ± 4a	15 ± 4a		10 ± 3a
	G. t. + BHT (10 mg/ml)	32 ± 10a	48 ± 8a		8 ± 3b	13 ± 3a		9 ± 3a
C_6H_{12}	*G. trabeum*	18 ± 5a		15 ± 3b			11 ± 3a	
	G. t. + BHT (1 mg/ml)	22 ± 7a		19 ± 5a			6 ± 1b	

Table 3. Mean (±SE) number of *Reticulitermes flavipes* workers in contact with paper disks treated with dichloromethane extracts of decayed red pine containing BHT, during successive five-minute intervals. The positions of 50 workers, tested individually in separate petri dishes, were recorded every 30 seconds, with each mean representing 10 successive 30-second observations. Means within each column followed by the same letter are not significantly different at the 0.05 level (ANOVA, REGW multiple F test).

Treatment	Number of Termites on Treated Papers (Individual Assays)			
	0–5 min	5.5–10 min	10.5–15 min	15.5–20 min
G. trabeum	28 ± 1a	17 ± 1a	14 ± 1a	12 ± 1a
G. t. + BHT (1 mg/ml)	12 ± 1b	12 ± 1bc	7 ± 1c	7 ± 1b
G. t. + BHT (10 mg/ml)	23 ± 1b	14 ± 1abc	10 ± 1b	7 ± 1b
G. t. + BHT (100 mg/ml)	17 ± 1c	14 ± 1ab	10 ± 1b	9 ± 1b
Dichloromethane Control	11 ± 1d	11 ± 1c	12 ± 1ab	12 ± 1a

air-dried from 15 to 135 minutes, and an *R. flavipes* worker (pseudergate older than the third instar as determined by size) placed at one end. The forward distance traveled on the trail in 30 seconds by the worker was recorded, and the distance traveled by 25 workers on 25 such trails per treatment compared by *t* test, or analysis of variance (ANOVA) and the Ryan-Einot-Gabriel-Welsch (REGW) multiple F test (SAS Institute 1987).

Orientation assays.—In addition to the trail-following assays, orientation assays using both individual workers and groups of ten workers were designed after those described by Grace (1989b) and Grace et al. (1989). In both individual and group assays, 100 μl of *G. trabeum* extract was applied by pipette to a 23 mm Whatman No. 3 filter paper disk. This disk was paired with a solvent-treated disk in a 5-cm diameter glass petri disk, and aired 15 minutes to evaporate the solvent. Either an individual termite worker or a group of ten workers was then placed in the dish, and their positions recorded every 30 seconds for 20 minutes.

In the individual assays, 50 workers were tested independently in separate petri dishes. The number of individuals in each treatment in contact with an extract-treated paper at each 30-second observation were compared for each five-minute interval (n = 10 observations per five-minute interval) by ANOVA and the REGW multiple F test (SAS Institute 1987). A series of control assays was included in which one of two equivalent solvent-treated disks was arbitrarily designated the "treatment" disk.

In the group orientation assays, 20 groups of ten workers were evaluated with each treatment. The 30-second observations were pooled over each five-minute interval (n =

Table 4. Mean (±SE) number of *Reticulitermes flavipes* workers in group assays in contact with paper disks treated with dichloromethane extracts of decayed red pine containing BHT, during successive five-minute intervals. The positions of 20 groups of 10 workers were recorded every 30 seconds and pooled for analysis, with each mean representing 200 observations. Means within each column followed by the same letter are not significantly different at the 0.05 level (ANOVA, REGW multiple F test).

Treatment	Number of Termites on Treated Papers (Group Assays)			
	0–5 min	5.5–10 min	10.5–15 min	15.5–20 min
G. trabeum	3.1 ± 0.1a	3.4 ± 0.2a	2.6 ± 0.2a	2.4 ± 0.1a
G. t. + BHT (1 mg/ml)	3.5 ± 0.1b	2.8 ± 0.1b	1.8 ± 0.1b	1.3 ± 0.1b
G. t. + BHT (10 mg/ml)	3.1 ± 0.1b	3.2 ± 0.1a	2.0 ± 0.1b	1.3 ± 0.1b
G. t. + BHT (100 mg/ml)	1.2 ± 0.1d	1.4 ± 0.1c	1.0 ± 0.1c	0.9 ± 0.1c
Dichloromethane Control	2.4 ± 0.1c	1.8 ± 0.1c	1.3 ± 0.1c	1.3 ± 0.1b

Table 5. Mean (±SE) number of *Reticulitermes flavipes* workers in contact with paper disks treated with a cyclohexane extract of decayed red pine or an extract containing 1 mg/ml BHT, during successive 5-minute intervals. Treated papers were aired either 15 or 60 minutes before the assay. The positions of 50 workers, tested individually in separate petri dishes, were recorded every 30 seconds, with each mean representing 10 successive 30-second observations. Treatment pairs (same time interval) within each column followed by an asterisk are significantly different at the 0.05 level (*t* test).

Time Interval	Treatment	Paper Aeration Time	
		15 min	60 min
0.5–5 min	*G. trabeum*	26 ± 2*	19 ± 1
	G. t. + BHT	20 ± 1*	20 ± 1
5.5–10 min	*G. trabeum*	18 ± 1*	15 ± 1
	G. t. + BHT	12 ± 1*	15 ± 1
10.5–15 min	*G. trabeum*	13 ± 1*	14 ± 1*
	G. t. + BHT	8 ± 1*	10 ± 1*
15.5–20 min	*G. trabeum*	15 ± 1*	14 ± 1*
	G. t. + BHT	6 ± 1*	8 ± 1*

200 observations per five-minute interval), and the mean numbers in contact with the extract-treated papers compared by ANOVA and the REGW multiple F test (SAS Institute 1987).

Both individual and group orientation assays, in which the test papers were air-dried 15 minutes, were performed with the dichloromethane *G. trabeum* extracts, containing either 0, 1, 10, or 100 mg/ml BHT. Cyclohexane *G. trabeum* extracts containing 0 or 1 mg/ml BHT were compared in individual assays in which the test papers were aired either 15 or 60 minutes. This latter procedure was adopted to preclude termite behavioral habituation to the test extracts (Grace 1989b) concealing differences between them.

Results and Discussion

Neither BHA nor BHT alone elicited trail-following by *R. flavipes,* and addition of BHA to the dichloromethane extract of wood decayed by *G. trabeum* completely suppressed trail-following (Table 1). Thus, BHA was not included in the individual and group orientation assays. With short aeration periods, addition of BHT did not affect the trail-following activity of the fungus extract (Table 2). Neither were any consistent effects on trail-following activity apparent with longer aeration periods. Addition of BHT did not arrest the observed decrease in extract trail-following activity with trail aeration time.

In the individual (Table 3) and group (Table 4) orientation assays, the BHT fortified extracts exhibited less activity than the dichloromethane *G. trabeum* extract, and decreased in activity over time. In several instances, the activity of the BHT extracts, particularly that containing 100 mg/ml BHT, fell below that of the solvent control, suggesting concentration-dependent repellency.

Results of the individual orientation assays with the cyclohexane extract (Table 5) were comparable to those obtained in the dichloromethane solvent system. Whether the test papers were aired 15 or 60 minutes, addition of 1 mg/ml BHT either made no difference in comparison to the activity of the stock *G. trabeum* extract, or resulted in a significant decrease in positive responses to the extract.

At the concentrations tested here, addition of BHA to *G. trabeum* extract resulted in a complete loss of behavioral activity towards *R. flavipes,* while BHT slightly decreased activity. Neither antioxidant appeared to provide protection to the fungal semiochemicals nor extend their longevity. However, the concentrations of behaviorally active compounds in the *G. trabeum* extracts were not determined, and very low concentrations of semiochemicals can elicit activity. More encouraging results might therefore be obtained with lower concentrations of antioxidants. This study indicates that BHT, which demonstrated a concentration-dependent repellency rather than complete suppression of activity, is the more

promising additive for use in such investigations.

Although studies with isomers and analogs of the identified dodecatrienol (Prestwich et al. 1984 and included citations) have demonstrated that the (*Z,Z*)-3,6-alkadien-1-ol functionality is more important than the conjugated 6,8-diene in eliciting trail-following, 6,8-dodecadien-1-ol also shows activity with *Reticulitermes* (J. K. Grace and M. Kim, unpublished results). Chemical protection of the identified semiochemical in *G. trabeum,* as well as other unidentified biologically active compounds in the solvent extracts, thus deserves further study as an approach to extending the field life of these potentially useful extracts.

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REDESCRIPTION AND IMMATURE STAGES OF *FICIOMYIA PERARTICULATA* (DIPTERA: CECIDOMYIIDAE), A GALL MIDGE INHABITING SYCONIA OF *FICUS CITRIFOLIA*

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Abstract.—Felt described *Ficiomyia perarticulata* and *F. birdi* from syconia of *Ficus aurea* Nutt. and *F. citrifolia* Mill., respectively, collected in southern Florida. We put *Ficiomyia birdi* Felt into synonymy because qualitative, quantitative and principal component analyses revealed no differences between Felt's type series of *F. perarticulata* and *F. birdi*. Felt's host plant record for *F. perarticulata* is probably wrong. After extensive sampling we conclude that the host-plant association of *Ficiomyia*, at least in Florida, is restricted to *Ficus citrifolia*. We redescribe the adult stages of *Ficiomyia perarticulata* and describe the immature stages for the first time. Adult males have considerably fewer antennal segments than females, which is otherwise unknown in gall midges. Other peculiarities include the development of a spatula in the second larval instar and the development of sexually dimorphic galls. Females cause longer, stalked galls and males sessile galls.

Key Words: *Ficiomyia*, *Ficus*, gall midge, immature stage, sexual dimorphism, emergence, principal component analysis (PCA), host-plant association, biogeography

One of the most striking examples of mutualism among phytophagous insects and their host plants is the association between figs and agaonid fig wasps. This association resulted in patterns of radiation that display remarkable co-evolved traits between the insects and figs. Fig wasps, which pollinate fig flowers and, in turn, use ovaries as larval development sites, are not the only group of insects that inhabit fig fruit. Other Hymenoptera, as well as gall midges, inhabit syconial galls (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926, Williams 1928, Barnes 1948, Condit 1969, Mani 1973). Felt (1922, 1934) erected the genus *Ficiomyia* for midges inducing pocket-like swellings within syconia of figs native to Florida, and described two species, *F. perarticulata* on *Ficus aurea* Nutt. and *F. birdi* on *Ficus citrifolia* Mill. (= *F. laevigata* Vahl). Both species are characterized by a large number of antennal segments, a reduced number of palpal segments, and peculiar male genitalia. Felt (1925) placed *Ficiomyia* in the tribe Dasyneuriariae: Gagné, in McAlpine et al. (1981) placed it, and all other Dasyneuriariae, in the tribe Oligotrophini. Like *Ficus*, *Ficiomyia* may extend into Florida from the Neotropics. Close relatives of the midge are unknown.

Because Felt described both species from a few poor and incomplete specimens, he

drew some erroneous conclusions concerning species differences and probably reported an incorrect host plant association. These errors became apparent after we analysed Felt's type series and a large sample of fresh specimens reared from authoritatively identified host plants. In this paper we redescribe *F. perarticulata* Felt and place *F. birdi* into synonymy. Extensive sampling of the purported host plant species native to Florida, and a comparison of both of Felt's type series with the midges we reared, show that his material, attributed to two species, is conspecific. We also described the immature stages of *Ficiomyia,* which, like the adults, possess some remarkable traits. Lastly, we described some aspects of the midge's biology, including emergence behavior and periodicity, mating, and the sex ratio.

Methods

We studied newly reared material and compared it with Felt's type series. Samples of syconia in various stages of development were dissected to determine the presence and abundance of midge galls. Immature stages were macerated in warm 80% lactic acid. First instar larvae were mounted in polyvinyl-lactophenol. Larvae of later instars and pupae were mounted in Euparal. Fruits of identified fig species were isolated in vials to rear adult gall midges. Adults were stored in 70% alcohol and eventually mounted in Euparal using the method outlined in Roskam (1977). Adult terminology follows McAlpine et al. (1981); for larval terminology, see Möhn (1955), and for pupal terminology Möhn (1961). All measurements were taken from slide-mounted material. The statistical methods are explained in the paragraph dealing with the comparison of new material with Felt's type series.

Behavioral observations were made in several locations in Dade and Monroe Counties, Florida. Sex ratio and periodicity of midge emergence from galls were studied in excised fruits which were isolated in plastic vials with mesh caps and ambient conditions.

Ficiomyia perarticulata Felt

Ficiomyia perarticulata Felt 1922: 5.
Ficiomyia birdi Felt 1934: 132. New Synonym.

For quantitative characters, see Tables 1 and 2.

Male.—*Head:* Eyes very large, holoptic, about 11 facets long at vertex; facets hexagonal, closely abutting one another (Fig. 1). Occiput diamond-shaped, largely covered with setae (Fig. 2). Antenna with 29–31 stalked flagellomeres, the fused first and second flagellomeres counted separately; node with a basal whorl of short, rigid setae and long, bent setae on horseshoe-shaped sockets scattered over its anterosubdistal surface, circumfila appressed, forming one complete basal whorl and a partial, anterodistally situated whorl, the two connected at the medial and lateral surfaces of the node (Fig. 6). Antennal plate and clypeus covered with many setae; labrum sclerotized; labium heart-shaped; labella hemispherical in lateral view, the distal half covered with rigid setae. Palpus 3-segmented, basal segment partly to completely fused with second, third segment variable in length; basal segment with two to six laterally-situated, long setae (Fig. 3).

Thorax: Scutum with four longitudinal rows of setae interspersed with scales. Scutellum with scattered setae and scales. Anepisternum with three groups of anterodorsally, anteroventrally and centrally situated setae and scales. Anepimeron with a central group of setae and scales. Legs densely covered with scales; claws toothed, teeth usually bifid, first tarsomere of all legs with pointed asetulose lateroventral projection (Fig. 5); empodia as long as or slightly longer than claws and twice as long as pulvilli (Fig. 4). Wing densely covered with scales, hyaline if scales absent, maculate if scales pres-

Table 1. Quantitative comparison of newly collected material with Felt's type series, males. All measurements are in μm, bold-printed values indicate ranges for Felt's series which exceed the ranges of the newly collected material. *, characters used for PCA.

Character	*perarticulata* new				*birdi* Felt		*perart.* Felt	
	N	Mean	cv %	Range	N	Range	N	Range
*he head	11	584	1.7	568–598	3	568–**637**	1	**617**
he antennal plate	11	198	3.6	184–208	3	**162**–184	1	184
nr flagellomeres	8	30	2.8	29–31	1	30	0	—
le antenna	8	2879	5.0	2684–3063	1	2716	0	—
*le 10 flagellomeres	11	1011	3.3	947–1074	2	917–1074	2	995–1074
le node 5. flagm.	11	68	7.0	63–77	2	68–70	2	63–75
wi node 5. flagm.	11	60	3.3	56–63	2	58–61	2	56–61
le stalk 5. flagm.	11	38	9.3	31–41	2	39–39	2	41–41
le seta node 5. fm.	8	255	10.0	223–300	3	290–**339**	2	227–**307**
le 3. palp segment	8	39	16.3	29–46	0	—	0	—
*le metafemur	11	1473	3.0	1421–1547	1	1532	2	1437–1468
le metatibia	11	1438	5.7	1295–1547	1	1437	2	1421–1500
le 2. metatarsus	11	1172	3.2	1105–1232	1	1232	2	1137–1263
le 5. metatarsus	11	229	4.8	205–237	0	—	1	221
wi wing	11	1061	3.6	979–1103	3	1074–**1232**	1	**884**
le vein R1	11	939	4.4	884–995	3	**1026**–**1184**	1	**1105**
*le vein R5	11	2367	2.6	2290–2495	3	**2605**–**2842**	1	2416
le basal branch Cu	11	687	4.9	647–742	3	647–**774**	0	—
le proximal br. Cu	11	1451	3.4	1374–1547	3	1515–**1768**	0	—
le distal br. Cu	11	812	4.8	758–900	3	**979**–**1011**	0	—
le gonocoxite	11	242	3.5	227–254	2	247–252	2	237–249
le lobe gonocoxite	11	128	7.5	104–138	2	116–121	0	—
wi gonocoxite	11	81	10.3	68–92	2	68–73	0	—
*le gonostylus	11	111	1.8	109–114	2	**99**–**121**	1	**116**
incisision cercus	11	96	12.9	80–121	2	97–102	2	92–94
incis hypopr	11	90	12.1	70–106	2	77–80	2	85–90

ent (fresh material) due to patches of broad, pigmented scales among patches of narrow, hyaline ones; R5 almost straight, declining at the very end towards wing tip and terminating slightly anterior to it, Cu forked, its branches straight (Fig. 8).

Abdomen: oblong cylindrical, yellowish and densely covered with broad, dark brown scales. Tergites 2–6 rectangular, with simple, uninterrupted, posterior rows of setae, lateral setae lacking, two trichoid sensilla on anterior margins, sclerotized parts covered with scales, tergite 4 about 2.5 times as wide as long, tergite 7 narrower, with double row of posterior setae, tergite 8 not sclerotized, indicated by some posterolaterally situated setae, trichoid sensilla present; pleura thickly covered with scales; sternites 2–7 rectangular, wider than long, setae in double rows on posterior margins, scattered along lateral margins and on anterolateral parts, a pair of closely placed trichoid sensilla on medioanterior margin, sclerotized parts with scattered scales, sclerite 8 narrower and without trichoid sensilla. Cerci rounded posteriorly, with rigid setae on posterior parts of both surfaces, arrangement of microtrichia in transverse, elongate patches anterodorsally, gradually changing to a scattered arrangement posteriorly, ventral surface with microtrichia in transverse rows; hypoproct variable, oblong, parallel-sided, and deeply emarginate, with microtrichia scattered on its dorsal surface and in transverse rows on the ventral surface, each lobe with two to three apical setae; gonocoxite oblong, narrowed at mid length, with a conspicuous apicoventral lobe, setae mainly on

Table 2. Quantitative comparison of newly collected material with Felt's type series, females. For further explanation, see Table 1.

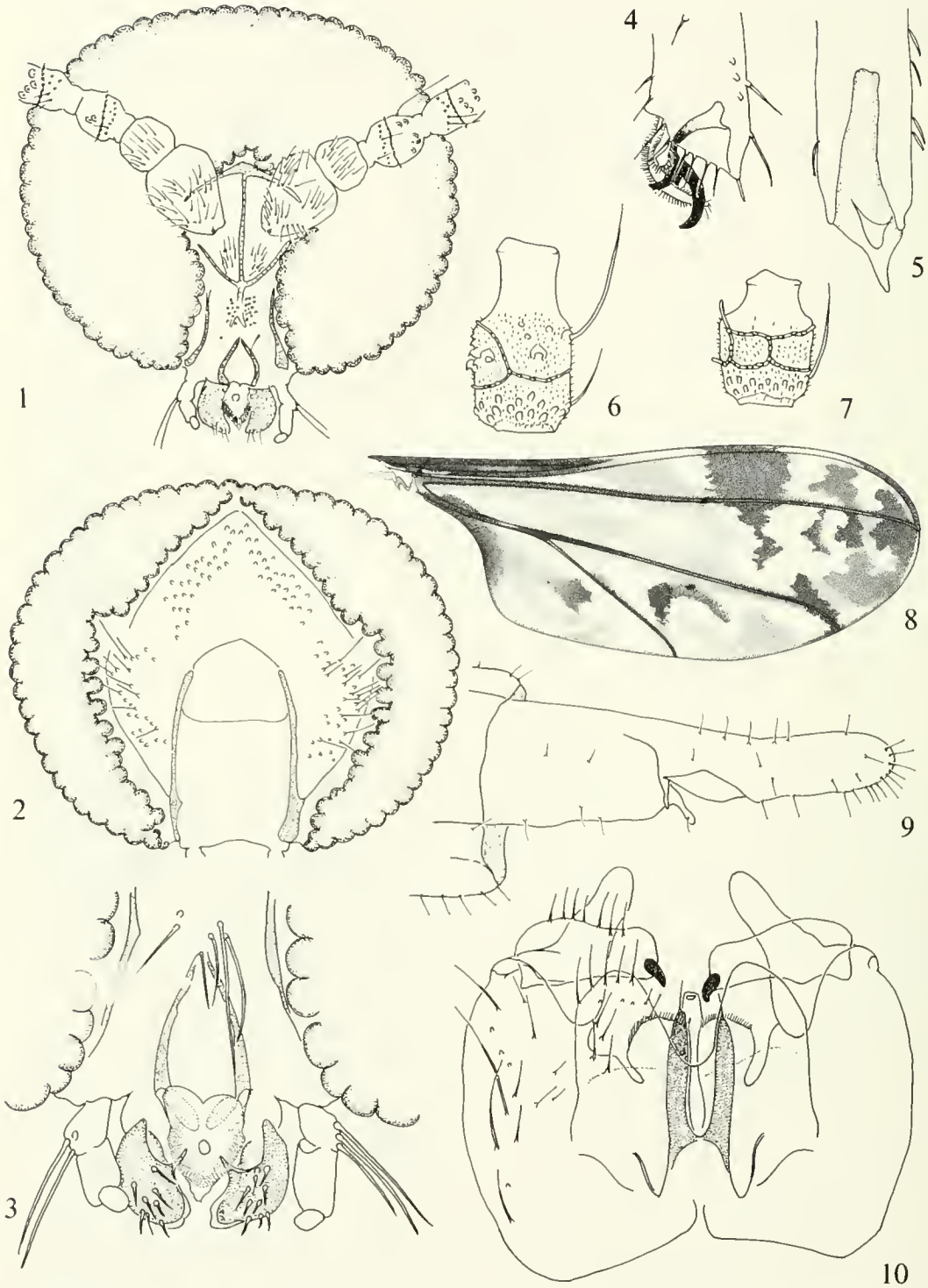
Character	*perarticulata* new				*birdi* Felt		*perart.* Felt	
	N	Mean	cv %	Range	N	Range	N	Range
*he head	11	584	3.0	559–608	2	**549**–568	4	568–608
he antennal plate	10	193	6.5	184–201	1	169	3	186–**203**
nr flagellomeres	9	38	2.2	37–39	0	—	2	39–39
le antenna	9	2482	5.8	2290–2700	0	—	1	**2921**
*le 10 flagellomeres	11	723	4.1	679–774	1	**790**	1	**821**
le node 5. flagm.	11	56	5.7	51–63	1	58	1	53
wi node 5. flagm.	11	57	4.8	53–61	1	58	1	**63**
le stalk 5. flagm.	11	23	10.9	19–24	1	**27**	1	24
le seta node 5. fm.	11	106	21.2	82–145	1	**148**	1	85
le 3. palp segment	10	41	27.0	24–58	0	—	1	34
*le metafemur	11	1503	5.4	1405–1642	2	1547–1579	3	1579–**1705**
le metatibia	11	1457	6.9	1342–1611	2	1547–1705	3	1611–**1721**
le 2. metatarsus	8	1153	8.4	963–1263	1	**1421**	0	—
le 5. metatarsus	7	229	5.0	221–237	0	—	0	—
wi wing	11	1192	3.8	1137–1263	2	1326–1405	2	1168–1326
le vein R1	11	1041	4.1	995–1105	2	1137–1231	2	1137–1200
*le vein R5	11	2626	3.7	2526–2779	2	**3047–3363**	2	2684–**3174**
le basal branch Cu	11	748	5.3	695–821	1	**916**	2	**679–868**
le proximal br. Cu	11	1652	4.9	1547–1753	2	**2053–2116**	2	1721–**2100**
le distal br. Cu	11	895	4.3	837–947	2	1105–1105	2	**995–1058**
le cercus	10	177	4.7	165–189	0	—	2	**143**–155
*he cercus	11	49	6.3	44–53	1	51	3	44–48
le hypoproct	11	28	17.1	22–34	1	29	3	29–**39**

distal part of dorsal surface and scattered over lateral and ventral surfaces; gonostylus cylindrical, blunt at apex, with curved, stout, apical tooth and with numerous setae, mainly on its lateral surfaces; mediobasal lobe about half as long as gonocercus, stout, blunt, with transverse, narrowly oblong patches of microtrichia; aedeagus slender, parallel sided, and distinctly longer than the mediobasal lobes (Fig. 10).

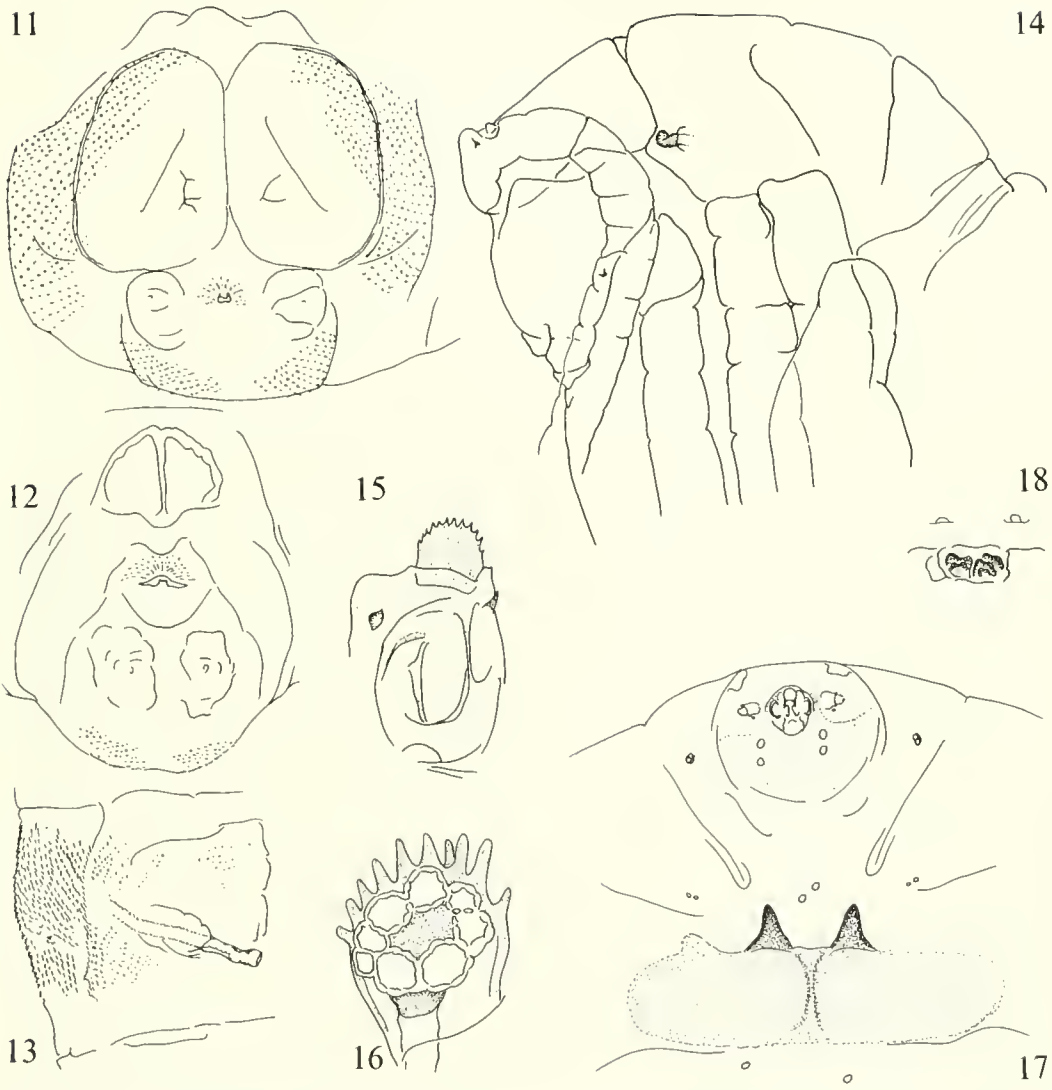
Female (characters not mentioned similar to those of the male).—*Head:* Antenna with 37–39 stalked flagellomeres; node with only basal whorl of short setae and complete, laterally and medially interconnected circumfila (Fig. 7).

Abdomen: ovoid, deep orange-red; spermathecae conspicuously pigmented. Ovipositor telescoped, abdominal segment 9 about 1.5 times as long as segment 8, with setae scattered all over its surface, the microtrichia in groups, forming a reticulate pattern, one pair of trichoid sensilla on anterolateral margin; segment 10 slightly longer than segment 9, with microtrichia in dense transverse rows; cercus oblong, with setae scattered over whole surface, the longer ones mainly distal, microtrichia densely scattered anteriorly, in more or less reticulate pattern posteriorly; hypoproct short, obtuse-triangular, with microtrichia in transverse rows (Fig. 9).

Pupa.—Color turning from creamy-white to yellowish in male and pink-orange in female. Apical and lateral spines on head, as well as lateral facial papillae, which are usually present in gall midge pupae, absent and indicated by blunt projections. One pair of trichoid sensilla on apical projections (Fig. 14). Thoracic horns absent, prothoracic spiracle protruding from its respective surface. Abdomen with five pairs of protruding spiracles, on segments 2–6, the pair of stigmata on segment 7 vestigial (Fig. 13). On seg-



Figs. 1–10. *F. perarticulata*, adult structures. 1, Male head, frontal. 2, Same, distal. 3, Mouthparts. 4, Detail of male hind fifth tarsomere. 5, Detail of distal part of male hind first tarsomere. 6, Male fifth flagellomere. 7, Female, same. 8, Male wing. 9, Ovipositor. 10, Male postabdomen, dorsal. 8, ×25. 1–2, ×100. 9–10, ×180. 6–7, ×240. 4–5, ×290.



Figs. 11–18. *F. perarticulata*, structures of immature stages. 11, Male pupa, distal view of ultimate abdominal segments. 12, Female pupa, same. 13, Male pupa, stigma and skin structures on sixth abdominal segment, lateroventral. 14, Male pupa, head and thorax, lateral. 15, Third instar larva, antenna. 16, Same, stigma on first thoracic segment. 17, Same, head, supernumerary segment and first thoracic segment with spatula, ventral. 18, Second instar larva, detail of spatula. 14, ×65. 13, ×100. 11–12, 17, ×150. 18, ×450. 16, ×725. 15, ×1450.

ments 2–6, three pairs of dorsal trichoid sensilla and one pair of pleural sensilla, the sublateral pair of dorsals closely situated to the intermediate pair. On segment 7, one pair of dorsals and one pair of laterals. Dorsal and lateral surfaces with pointed setulae, ventral surface glabrous. Male pupa with two large posterior convexities in which the gonocoxites develop; female pupae with these cavities vestigial (Figs. 11–12).

Third (final) instar.—Body obconic, with broad thorax and upwardly curved, gradually narrowing abdomen, creamy-white; segmentation as usual for gall midge larvae and consisting of head (h), supernumerary segment (ss), three thoracic (t1–3), nine ab-

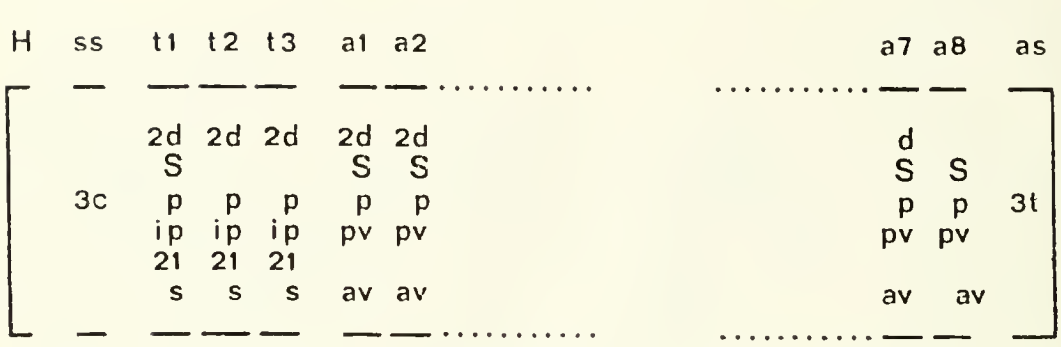


Fig. 19. *F. perarticulata,* diagram of pattern of papillae and tracheal system of third instar larva. a1–8, abdominal segments. as, anal segment. av, anterior ventral papilla. c, collar papilla. d, dorsal papilla. h, head. ip, interior pleural papilla. l, lateral papilla. p, pleural papilla. pv, posterior ventral papilla. S, stigma. s, sternal papilla. ss, supernumerary segment. t, terminal papilla. t1–3, thoracic segments.

dominal (a1–9), of which the final one is the anal segment (as). Body length 1850–2520 μm, width 850–1410 μm, head capsule width 123–157 μm, width between antennae 53–70 μm. Head capsule flat, weakly sclerotized, antennae truncate with sclerotized, plumose appendages (Fig. 15); thoracic surface glabrous, anteroventral surface of a2–a7 with about 25 transverse spinule-rows, a8 with such rows on its posteroventral surface. Spatula transverse, bilobed, the lobes acute; stalk not differentiated. Spatula height 94–126 μm, width 236–314 μm, height of lobes 34–46 μm, distance between tips 48–85 μm (Fig. 17). Respiration peripneustic, with spiracles on t1 and a1–a8; spiracles with oblong sclerotized outgrowths (Fig. 16). Papillae, unless indicated otherwise, without setae; pattern of papillae; three pairs of lateral collar papillae, the papillae of two of these pairs abutting (Fig. 17); thoracic segments with one pair of sternal papillae each, the pair on t1 abutting and confined by the spatula lobes (Fig. 17), two pairs of abutting laterals with short setae, one pair of interior pleurals, two pairs of dorsals; segments a1–a7 with one pair of anterior ventral papillae, one pair of posterior ventrals, one pair of laterals and two pairs of dorsals; a8 with dorsal papillae missing; anal segment with usually three pairs of terminal papillae, anal papillae absent (Fig. 19). N = 10.

First instar.—Body ellipsoid, transparent. Body length 588–735 μm, width 225–254 μm. Head capsule width 33–41 μm, flattened, with truncate antennae. Body surface glabrous with patches of minute spinule-rows on dorsal and ventral surfaces. Spatula absent. Respiration apneustic with a pair of vestigial spiracles on abdominal segment 8. All papillae without setae except the pleural pair on abdominal segment 8. Pattern of papillae basically as in third instar; the pair of pleural papillae on abdominal segment 8 very distinct and with short setae. N = 4.

Second instar.—Body ellipsoid, creamy-white. Body length and width not defined because of the poor condition of the material. Head capsule width 87 μm, head capsule convex, with truncate antennae. Body surfaces as in first instar. Spatula present, bilobed, stalk not differentiated, width 17 μm, between lobes 7 μm (Fig. 18). Respiration peripneustic, with spiracles situated as in third instar, width of first thoracic spiracle 10 μm. Pattern of papillae as in third instar. N = 1.

Gall.—Barnes (1948) described the gall as an enlarged seed capsule which becomes abnormally lengthened. However, because the young gall may bear one to three flowers on its exterior, the gall must be considered a pocket-shaped outgrowth of the receptacle (Fig. 20). The associated flowers are gradually reduced as the gall matures. One larva is present per gall. The first instar is oriented

with its head towards the syconial cavity and is completely enclosed by the gall tissue; the head is traceable by a pair of dark eyespots (Fig. 21). A gall chamber becomes distinct when the larval spatula develops. At the late pupal stage a conspicuous 'crown,' with a central window-pit, grows from the top of the gall on the fruit surface. Often, two or three galls are concentrated around one window-pit. One to several crowns occur per galled fruit.

Two shapes are distinguished in mature galls (Fig. 22): shorter, sessile galls with the gall chamber situated close to the window-pit, and longer, stalked galls with a distinct constriction between gall chamber and window-pit. Males developed exclusively in the sessile galls, and females in the stalked galls. This was determined by dissection of pupae from galls (N = 15 per gall type), and dissection of galls after emergence of adults (N = 30 per gall type). Such a dimorphism has also been reported by Coutin and Riom (1967) for *Mikiola fagi* Hartig on beech in Europe.

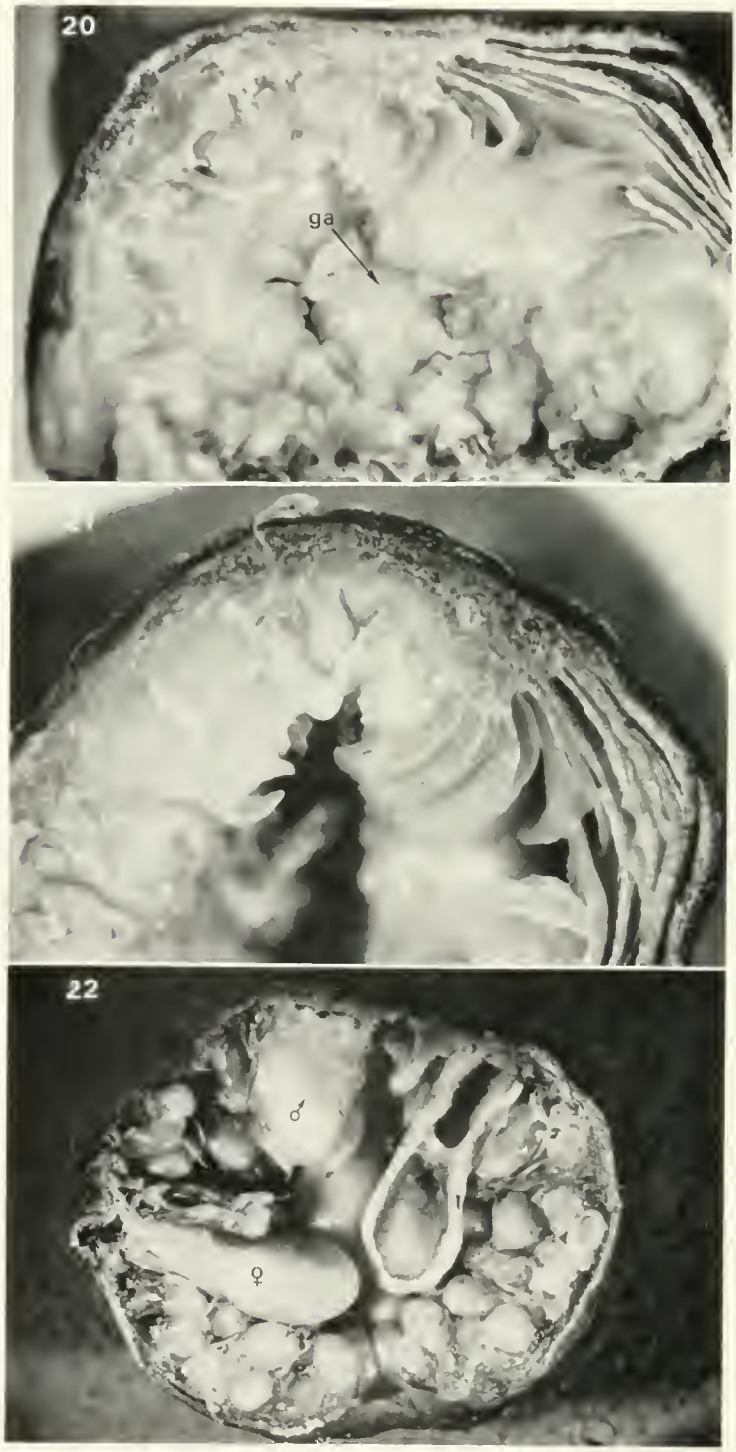
Types.—Felt did not designate holotypes from among his type series. Lectotypes are therefore designated here by one of us (JCR). For *F. perarticulata* slide "a," male, with left hand label "Lectotype, design. by J. C. Roskam 1989"; for *F. birdi* the slide marked with "type" by Felt, male, remounted by R. J. Gagné, again with left hand label "Lectotype, design. by J. C. Roskam 1989." All specimens of both Felt series belong to the New York State Museum at Albany and are now on indefinite loan to the Systematic Entomology Laboratory in Washington, D.C. The specimens we mounted have been deposited in U.S. National Museum in Washington.

Comparison of New Material with Felt's Type Series

The type series of *F. perarticulata* consists of 10 slides with specimens or fragments mounted in Canada balsam. Felt (1922) described the specimens as "somewhat broken in transit and as a consequence, the descriptions . . . are not complete in certain details." All slides are labeled "Ficiomyia perarticulata Felt on Ficus aurea Miami, Fla. Feb. 9 '22 Type a32128." On two of these slides, labeled by one of us (JCR) with "male a" and "male b," a male is mounted, both with incomplete antennae and shriveled heads and legs. Five slides, labeled with "female a"–"female e," bear incomplete females. All this material was cleared before mounting. A slide labeled "f" contains two wings of different sizes, apparently taken from specimens before clearing; a slide labeled "g" contains a complete female flagellum in shriveled condition. Finally, a slide marked "h" contains a mixture of incomplete male and female flagella, legs, and the thorax and gaster of a female fig wasp, *Pegoscapus* sp. (species identification not possible without the head). The type series of *F. birdi* Felt consists of three slides with a male on each and two slides with a female on each. One male and one female are marked "type"; all slides are labeled "Ficiomyia birdi Felt Florida 1933." The male that we designate as lectotype has been cleared and remounted by R. J. Gagné, Washington, D.C. (R. J. Gagné, in litt.). Felt's (1934) statement about the number of antennal segments is based on material of the male marked "b" by JCR. All material, specimen "b" excepted, has incomplete antennae and legs and shriveled palpi.

The lobed gonocoxites and the high number of stalked antennal segments in both sexes, characters on which the genus *Ficiomyia* was erected, are distinct in the material of both type series. The statements "palpi probably uniarticulate" (Felt 1922) or "palp consisting of one, slender, rather long segment" (Felt 1934), which are used to distinguish *Ficiomyia* (Felt 1925, Gagné in McAlpine et al. 1981) are not correct. These must be replaced by "palpi usually 3-segmented, with the first and second segments partly to completely fused."

Examination of new material revealed that



Figs. 20–22. Longitudinal sections of infested *F. citrifolia* syconia. 20, Gall with reduced flowers on its exterior (ga). 21, Gall with first instar gall midge larva. 22, Syconium with two stalked (female) and one sessile (male) gall. 22, ×8. 20–21, ×12.

the species differences presented by Felt (1934) for *F. perarticulata* and *F. birdi* are not valid. The difference in body color is apparently due to different clearing of the material. The fuscous markings on the wings reported by Felt (1934) of *F. birdi* (caused by a thick layer of scales) are absent in the material of *F. perarticulata,* but this is probably an artifact: the scales are easily dislodged in alcohol-stored material. The most striking difference reported by Felt, however, concerns the number of antennal segments. He apparently used a complete female antenna for his description of *F. perarticulata,* whereas he used the antenna of a male in his description of *F. birdi.* This difference in the number of antennal segments, though, is not due to a species difference but to sexual dimorphism. This is the first record of considerably fewer flagellomeres in males than females in Cecidomyiidae. Male cecidomyiids generally have as many or a few more flagellomeres than females. *Ficiomyia* is, therefore, remarkable among gall midges (for a review, see Mamaev 1968). Finally, we doubt the identification of the host plant of *F. perarticulata.* For a discussion, see the section on host plant associations.

Because we found no qualitative characters to differentiate between the two species, we sought differences by using quantitative analysis. The quantitative traits are listed in Tables 1–2. Although both of Felt's series comprise considerably less material than the material we reared, his material is more variable. His midges are generally larger, but in eight cases from both series some characters exceeded both the lower and upper boundaries of the ranges set by our material. Therefore, although our material should be conspecific with one of Felt's series, the difference between the Felt material and our midges is larger than the difference between Felt's series. Based on this analysis, we again find no evidence to support the view that *F. perarticulata* and *F. birdi* are different species.

With principal component analysis (PCA) it is possible to analyse several characters simultaneously; the technique therefore allows a more accurate judgment on the status of *F. perarticulata* and *F. birdi.* For a description of the technique and an outline of its possibilities, see Pimentel (1979). Among its attributes, PCA results in a graphic representation of specimens in a coordinate system with axes that show zero intercorrelations and to which the original characters (by measured values of the data matrix) have contributed proportionally to their variation. Put otherwise, the original axes, representing the characters, are rotated while the original relationships among the data points, representing the specimens, are maintained.

If *F. perarticulata* and *F. birdi* are different species, they should take different positions in a PCA hyperspace. The members of one of such supposed species should occupy closer mutual positions than members of a different species. The data matrix consists of values measured for the specimens we reared. Because the technique does not allow missing values, and missing values are frequent in Felt's type series, we represented the type series by mean values (Tables 1, 2). We are aware of the flaws of this decision but, given the poor condition of the material, it was our best option. Therefore, apart from the matrix of 11 specimens per sex we include two 'type representatives,' one for *F. perarticulata* and one for *F. birdi,* again per sex.

The data matrix is standardized (means zero, standard deviations 1) because the characters used are of a different size order (Tables 1, 2). The values for Felt's material have been standardized using the mean values and standard deviations from the characters as listed in Tables 1 and 2. All characters were tested for normality. A PCA technique constrains the number of characters which can be used relative to the number of specimens, and, in our case necessitates a low 'within species variation.'

We therefore chose a limited number (5) of characters showing a low coefficient of variation (Tables 1, 2). We selected these characters from different body regions to avoid combinations of characters with high intercorrelations (e.g. different parts of one leg). The PCA was done for males and females separately.

Results.—Males (Fig. 23). The type series of *F. perarticulata* (P) and *F. birdi* (B) are excentrally situated: both represent large midges. The *F. perarticulata* representation (P) is nearest to the centroid, even closer than specimen marked i. The latter specimen, like all others (a–k), supposedly belongs to *F. birdi* on the basis of host plant association. The *F. birdi* representation (B) is situated farthest from the centroid, but, on the other hand, is so closely situated to specimen i that we cannot assign it to a separate species. For females (Fig. 23) the result is even clearer: here both *F. birdi* and *F. perarticulata* representations are excentric, but mutually very close. Therefore we must conclude again that *all* material, i.e., Felt's type series *and* our material, is conspecific, and *F. birdi* must be put into synonymy for reason of priority.

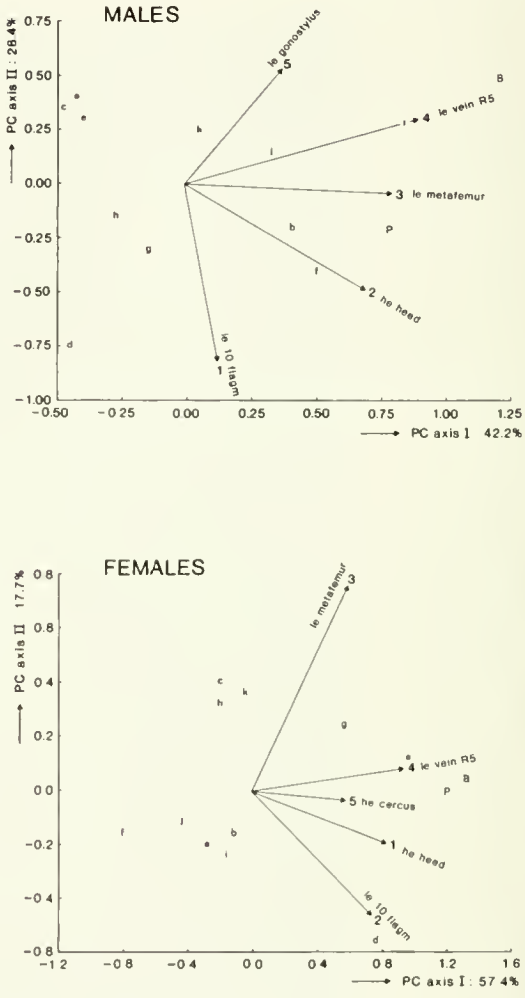


Fig. 23. Principal component analysis of adult characters. The vectors indicate amount and direction in which the separate characters attribute to the position of the specimens. a–k, Newly reared specimens. B, Representation of *F. birdi*. P, Same, *F. perarcticulata*. For further explanation, see text.

Distribution and Host Plant Association

Ficus aurea, the Florida strangler fig, and *F. citrifolia*, the shortleaf fig, are native to Florida. The Florida strangler fig is more abundant and occurs also on the Bahama Islands. The shortleaf fig is restricted in Florida to hammocks in the southernmost part and the Florida Keys, and occurs also in the Bahamas and the West Indies (Elias 1987). Although we examined many samples of *F. aurea*, we never found *Ficiomyia* or its parasitoid, *Physothorax bidentulus* Burks, in this fig species (there is one record of *P. bidentulus* from *F. aurea*, in Burks (1969), but it is from the same collection from which *F. perarticulata* was described). D. McKey, botanist at the University of Florida at Miami has also never found the conspicuous *Ficiomyia* galls in syconia of *F. aurea* (pers. comm.). The record of *Ficiomyia* on *F. aurea*, therefore, was probably due to a misidentification of the host plant. The host plant of *F. perarticulata* has also been erroneously listed as *F. carica* in Gagné (1989).

We examined the following samples: *Ficus aurea*, Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 147 syconia,

diameter 5–8 mm, two kinds of ovaries, small and large, containing different species of fig wasps, the species in the larger ovaries containing *Physothorax;* Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 50 syconia, diameter 5–8 mm, two sizes of fig wasp-containing ovaries, the larger containing *Physothorax;* Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 50 syconia, diameter 5–6 mm, ovipositing agaonids, no size differences among ovaries; Lee Co., Sanibel Island, 3-25-89, leg. H. Nadel and J. C. Roskam, 100 syconia, diameter 5–9 mm, small and large ovaries, one *Physothorax russelli* Crawford. Monroe Co., No Name Key, 9-17-88, leg. H. Nadel, 15 syconia, diameter 7–8 mm, some with many fig wasps, no midge galls. Monroe Co., Key Largo, 9-12-88, leg. H. Nadel, 46 syconia, diameter 5–8 mm, some with remnants of founding fig wasp females, others with almost emerged fig wasps, no midge galls.

Ficus citrifolia, Dade Co., Miami, 6-24-88, leg. H. Nadel and M. Matthews, 49 syconia, diameter 7–10 mm, with fig wasp remnants; 31 syconia with 80 galls, second and third instar midge larvae, midge pupae and emerged galls, third instar parasitoid larvae and parasitoid pupae; Dade Co., Homestead, 3-13-89, leg. C. Campbell, 200 syconia, diameter 7–11 mm, 20 of these syconia with one to five *Ficiomyia* galls each. Midge larvae parasitized by *Physothorax bidentulus* Burks, pupae by an unidentified chalcidoid. Furthermore we reared species of *Pegoscapus* (Agaonidae), *Colyostichus, Idarnes* (Torymidae), and an eurytomid, probably a *Syceurytoma.* The latter form was also dissected from galls. Heavy mortality of wasps was caused by larvae of a staphylinid beetle and a few ant species; Dade Co., Miami, 3-15-89, leg. H. Nadel and J. C. Roskam, 200 syconia, diameter 5–8 mm, 30 galls, induced by *Ficiomyia,* larvae in second and third instar, parasitoids absent; Monroe Co., No Name Key, 8-7-88, leg. H. Nadel, 30 syconia, diameter

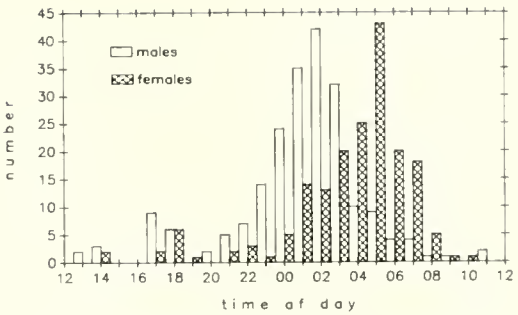


Fig. 24. Distribution of emergence of adult *F. perarticulata* from syconia of *Ficus citrifolia* in southern Florida. Data were combined from four days of hourly observation during April and May 1989.

8 mm, with remnants of fig wasps and agaonid larvae, no galls; Monroe Co., No Name Key, 9-17-88, leg. H. Nadel, 17 syconia, diameter 8–10 mm, with fig wasp remnants, many galls with midge pupae and emerged adults; Monroe Co., Key Largo, 9-12-88, leg. H. Nadel, 22 syconia, diameter 4–5 mm, too young for ovipositing fig wasps; five syconia, each with one gall, one syconium with three galls, all with first instar midge larvae; Monroe Co., Key Largo, 3-28-89, leg. H. Nadel and J. C. Roskam, 30 syconia, galls absent, two kinds of ovaries containing agaonid and torymid wasps.

Adult Emergence from Galls

The formation of the crown-like ridge around the opening of the gall begins about two days before eclosion of *F. perarticulata.* The fig skin splits, exposing the whitish tissue of the syconial wall, and curls outward radially to form a crown around the exit area. The tissue within the base of the gall becomes moist and vicid. The pupa pushes its way head first to the gall exterior and comes to rest with about three-quarters of its length protruding from the fig surface. The adult ecloses after a few minutes, leaving the pupal skin partly embedded in the crown, and rests hanging from the side or bottom of the fig by its front and middle legs. The wings are fully expanded within

five minutes and are capable of sustained flight within an hour after eclosion.

Daily emergence within a population is periodic, with a minor peak in late afternoon and a major peak during the night, and with males tending to emerge earlier than females during the major peak (Fig. 24). Within a single fig, emergence of all adults usually spans a few days, and may span even weeks, as suggested by our observations of second instar larvae in figs with already emerged galls.

Emergence occurs throughout the year in Florida, as *F. citrifolia* trees fruit asynchronously in relation to each other and thus afford year-round development by the gall midges. This scenario probably prevails over the entire range of the midge.

Mating

Mating probably occurs on or around the tree from which adults emerged. Females extrude their ovipositors directly after eclosion, apparently to emit pheromones. On three evenings around sunset we observed males, solitary and in small groups, flying in zigzag motion towards and around tips of branches. Males also frequently landed on fruits and leaves. We observed only one mating pair, which was on a fig at 17:45 on 6 December. The female, however, was captured by an ant either before or during copulation. The male continued to hang, head-down, by its terminalia for five minutes before disengaging from the female.

Sex Ratio

Both sexes may inhabit one fig. The sexual dimorphism in gall shape allowed us to determine midge sex ratio before mortality due to parasitism. In one sample of 13 fruits with 134 galls, 69 galls were male (sessile) and 65 were female (stalked), which is essentially a 1:1 ratio; however, in a sample of 50 fruits from a different location, 61 were male and 24 were female, which is highly male-biased (Chi-square = 16.11; $P < .005$). The sex ratio of emerged adults was studied in four other locations. Collection 1 yielded 32 adult males and 35 females; collection 2 yielded 32 males and 20 females; collection 3 yielded 70 males and 46 females; and collection 4 yielded 88 males and 81 females. The sex ratio in collection 3 deviated significantly from 1:1 (Chi-square = 4.97; $.025 < P < .050$). Apparently, sex ratio of *F. perarticulata* varies from equality to male-biased.

Syconial Gall Midges in Other Geographic Areas

If close relatives of *Ficiomyia* exist, we would expect them in syconia of figs occurring elsewhere. Docters van Leeuwen-Reijvaan and Docters van Leeuwen (1926) listed 28 kinds of galls from Malaysian figs on leaves, stems, aerial roots, and three kinds in syconia. Samples of these fruit galls, dried and in alcohol, have been deposited in the Rijksherbarium at Leiden, the Netherlands. None of the syconia of this material bear galls of the type induced by *Ficiomyia*. We dissected one mature larva from a syconium. This larva differs in many respects from *Ficiomyia* larva and probably belongs to the tribe Cecidomyiini. Barnes, in Williams (1928), described two species, one cecidomyiine and the other an asphondyliine, from fruits of figs native to the Philippines. These species, together with a cecidomyiine occurring in India, have also been listed in Barnes (1948). Although seven species of figs occur in Japan (Ohwi 1965), no cecidomyiids have been reported from them (Yukawa 1971). Finally, Mani (1973) distinguished eight kinds of leaf galls, but none is induced by Oligotrophini.

Two females, undoubtedly belonging to *Ficiomyia*, have been collected in a light trap in Dominica (West Indies, Clarke Hall, 1–10 February and 1–10 March 1965, leg. W. W. Wirth). The sole complete flagellum yields a count of only 33 flagellomeres and the hypoproct is slightly longer (41 μm) in one specimen. All remaining measurements are within the ranges given for *F. perarticu-*

lata. Because of the low number of flagellomeres this material might belong to a new species. More material and host data are required, though, to draw a conclusion and to provide a formal description.

Possible *Ficiomyia* parasitoids, in the genus *Physothorax,* have been described from Brazil, reared from big, stalked galls in the syconia of *F. doliaria* Mart. (Mayr 1885, 1906, Müller 1886). We cannot conclude, however, whether this indicates the presence of *Ficiomyia* in Brazil, since *P. russelli* Crawford and *P. pallidus* Ashmead also emerge from large, stalked galls in *F. aurea*. These galls are not induced by *Ficiomyia,* but probably by torymid sp. The genus *Physothorax* is not known outside the New World (Bouček et al. 1981). Hence, although our data are incomplete, there is no evidence that *Ficiomyia* or its parasitoid, *Physothorax,* occurs outside the New World. *Syceurytoma* has been described from African material (Bouček et al. 1981), but again there is no evidence that any of its species are associated with *Ficiomyia*.

Acknowledgments

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TWO NEW SPECIES OF *METAJAPYX* (DIPLURA: JAPYGIDAE) FROM TENNESSEE

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Abstract.—Two new species of Japygidae from eastern Tennessee are described and illustrated. ***Metajapyx heterocercus*** n. sp. exhibits sexual dimorphism of the cerci and chaetotaxy of the tenth abdominal tergum, and ***Metajapyx magnifimbriatus*** n. sp. exhibits only 30 antennal segments. Both sexual dimorphism and the reduced number of antennal segments are new characters of the genus in the United States.

Key Words: Diplura, Japygidae, *Metajapyx*, taxonomy

The genus *Metajapyx* Silvestri is represented in North America by eight eastern species (Smith and Bolton 1964). Recently, Rathman et al. (1988) illustrated a japygid from eastern Washington State as a *Metajapyx* sp.; some generic criteria for the genus *Metajapyx* were not reported for those specimens and therefore, further study is required to determine their generic placement.

Although two species of *Metajapyx* are quite widespread and frequently encountered (*M. subterraneus* [Packard] and *M. steevesi* Smith and Bolton), the other six species are locally distributed and rarely encountered. During intensive collection of *Metajapyx* spp. in the eastern United States for the purpose of revisionary studies we found two new *Metajapyx* species from eastern Tennessee. The objective of this paper is to describe and illustrate these new species.

MATERIALS AND METHODS

All specimens were cleared and stained in Essig's Aphid Fluid (Wilky 1962) and double stain (1 part 5% aqueous lignin pink and 5% aqueous acid fuchsin to 10 parts of Essig's Aphid Fluid), then mounted in polyvinyl alcohol-lactophenol to further clear and expand the specimens, and dried in an oven (60°C) for two days. Measurements and illustrations were made with an ocular micrometer and a Nikon phase-contrast microscope equipped with a drawing tube or a Unitron stereo microscope. Body length measurements were made from the basal articulation of the antennae to the apex of the cerci. Measurements are presented as a mean followed in parentheses by the range.

Because the distinctions among certain taxonomic characters used to describe Japygidae are sometimes vague it may be helpful to define the more salient of these. The following definitions are those of Smith (1962): M = larger macrosetae of the body set in reinforced setal sockets, so as to move in a plane parallel to the body; m = medium-sized sub-macrosetae usually set in simple setal sockets; Microsetae = minute setae visible only under high magnification, always set in simple setal sockets; Friction

setae = a type of microseta with large sockets that occur in groups where the body integument folds or moves upon itself; Calcar setae = two setae at the ventral apex of a tibia which may be thicker or more robust, but no longer than other tibial setae; Apotome = the anterior sclerite of an abdominal sternum. For a more complete treatise of japygid terminology one should refer to Smith (1962), Pagés (1952), and Steinmann and Zombori (1984).

Another potentially important taxonomic character of japygids is cercal chaetotaxy. This character has been either ignored or used only sparingly in japygid taxonomy, yet it appears to be useful at the generic and specific levels. In this paper we propose a new scheme to describe the cercal chaetotaxy of the genus *Metajapyx*. The cercal setae are arranged into four general categories: the lateral setae (L), the dorsal setae (D), the ventral setae (V), and the postdental margin setae (P). Within each group, setae are numbered from proximal to apical, and given relative size descriptions (long, short or minute). In this paper cercal chaetotaxy is used to help distinguish closely related species.

Metajapyx heterocercus Muegge and Bernard
NEW SPECIES
(Figs. 1a–f, 2a–d; Table 1)

Females.—Body length 12.1 (9.3–14.5) mm. Entire body and head yellowish-white, except for median sclerotized area at apex of epicranial and postoccipital sutures, and tergites VI through X, which are progressively more sclerotized posteriorly. Cerci heavily sclerotized.

Antennae: Thirty-two segmented and heavily setose, setae arranged in two irregular whorls, the basal whorl alternating as simple and hooked setae on segments 7 to 31 (Fig. 1a); terminal segment with 6 placoid sensilla arranged with 2 in basal whorl, 4 in apical whorl; lateral proliferation of setae occurring on segments 15 to 19; trichobothria present on segments 4–6 in a 3,5,5 pattern and nearly as long as longest seta on segment.

Head: Numerous M, m, and microsetae; admental plate with 35+35 (29–42) m + microsetae; prementum with 27+27 (30–43) m + microsetae, most restricted to anterior half of sclerite; postmentum 1+1M, 1+1m, and 19+19 (17–20) scattered microsetae; submentum 1+1M, 4+4m, and 10+10 (8–12) scattered microsetae. Labial palp conical with one or two apical sensory cones and 11+11 (10–12) setae, the longest slightly longer than palpus. Terminal segment of maxillary palpus with 22 (20–27) setae, the longest as long as the segment; galea with 3 (3–4) external setae in a row, thumb of galea sclerotized, with 3 long sensory cones and 9 (6–11) short sensory cones; lacinia falciform and heavily sclerotized, all five laminae pectinate (Table 1), with a small basal spur between laminae III and IV.

Thorax: Pronotum 5+5M, 5+5m, and scattered microsetae; prescutum 1+1M and posteromedian and posterolateral groups of friction setae; mesonotum 6+6M, 7+7m, and scattered microsetae (Fig. 1b); prescutum 1+1M; posteromedian and lateral margin with friction setae; metanotum 5+5M, 5+5m, and scattered microsetae.

Legs: Pro-, meso-, and metacoxae each with a row of friction setae near apex of segment; dorsal base of trochanter with a circular group of friction setae; dorsal apex of femur with a row of 4 long setae; ventral apex of tibia with 2 calcar setae, one much longer than the other; tarsus with two ventral rows of 4–6 large setae becoming more robust distally. Additional setae on all segments scattered, most restricted to distal ⅔ of segment. Empodium minute on protarsus and becoming progressively larger on meso- and metatarsi, metatarsal empodium subequal to pretarsus.

Abdomen: Prescutum 1+1M and scattered friction setae; scutum 1+1M and scattered friction setae. Tergite II 3+3M, 2+2m, and scattered microsetae; anteromedian pair

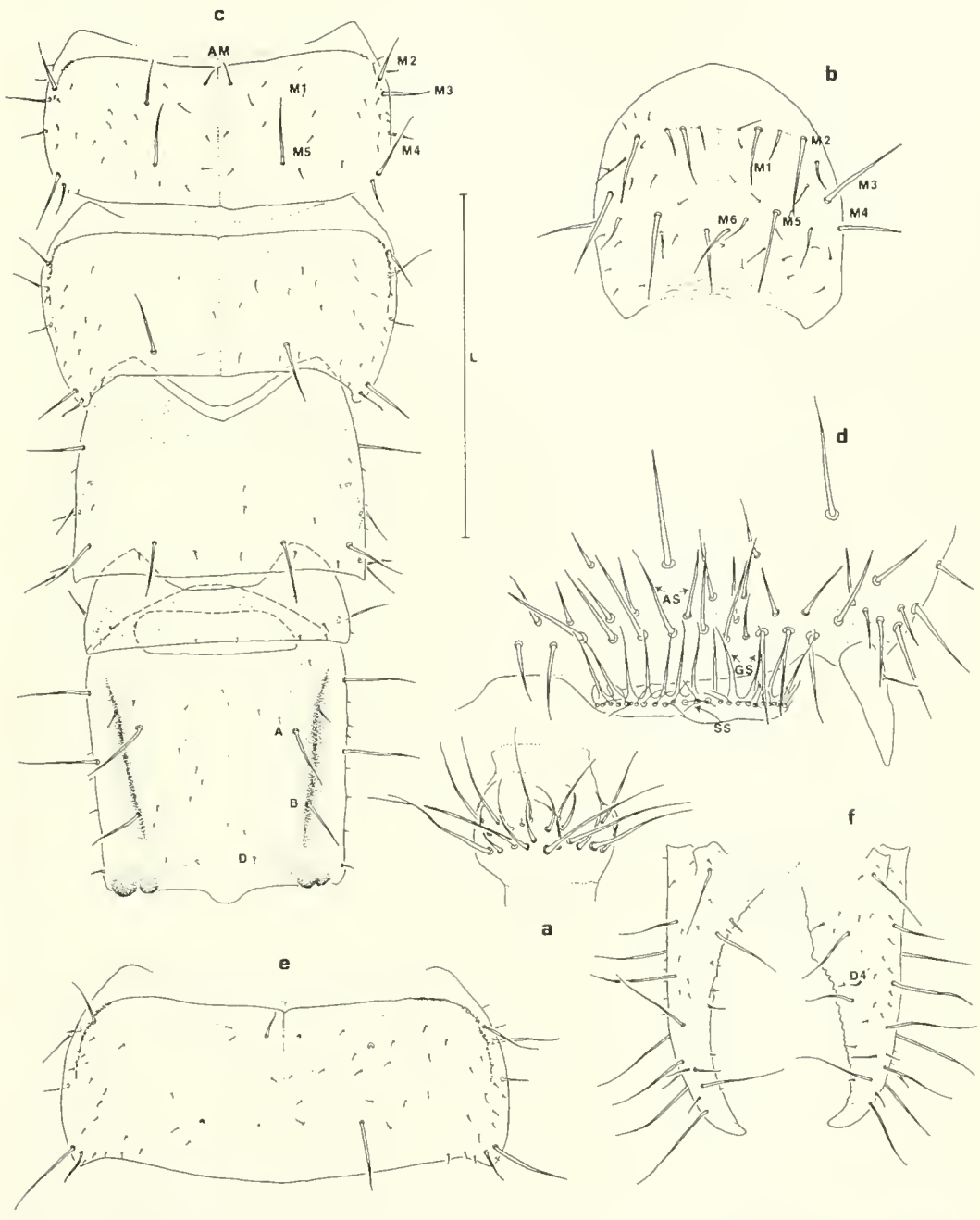

Fig. 1a–f. *Metajapyx heterocercus*. a, 14th antennal segment, L = 0.25 mm. b, Mesothorax, L = 1.0 mm. c, Tergites VI–X, L = 1.0 mm. d, 1st abdomenal sternum, L = 0.25 mm. e, Tergite VI of male, L = 1.0 mm. f, Cerci of male, L = 1.0 mm. Terms: AM, anteromedian pair of setae; M, macroseta; AS, antecedent setae; GS, glandular setae; SS, sensory setae.

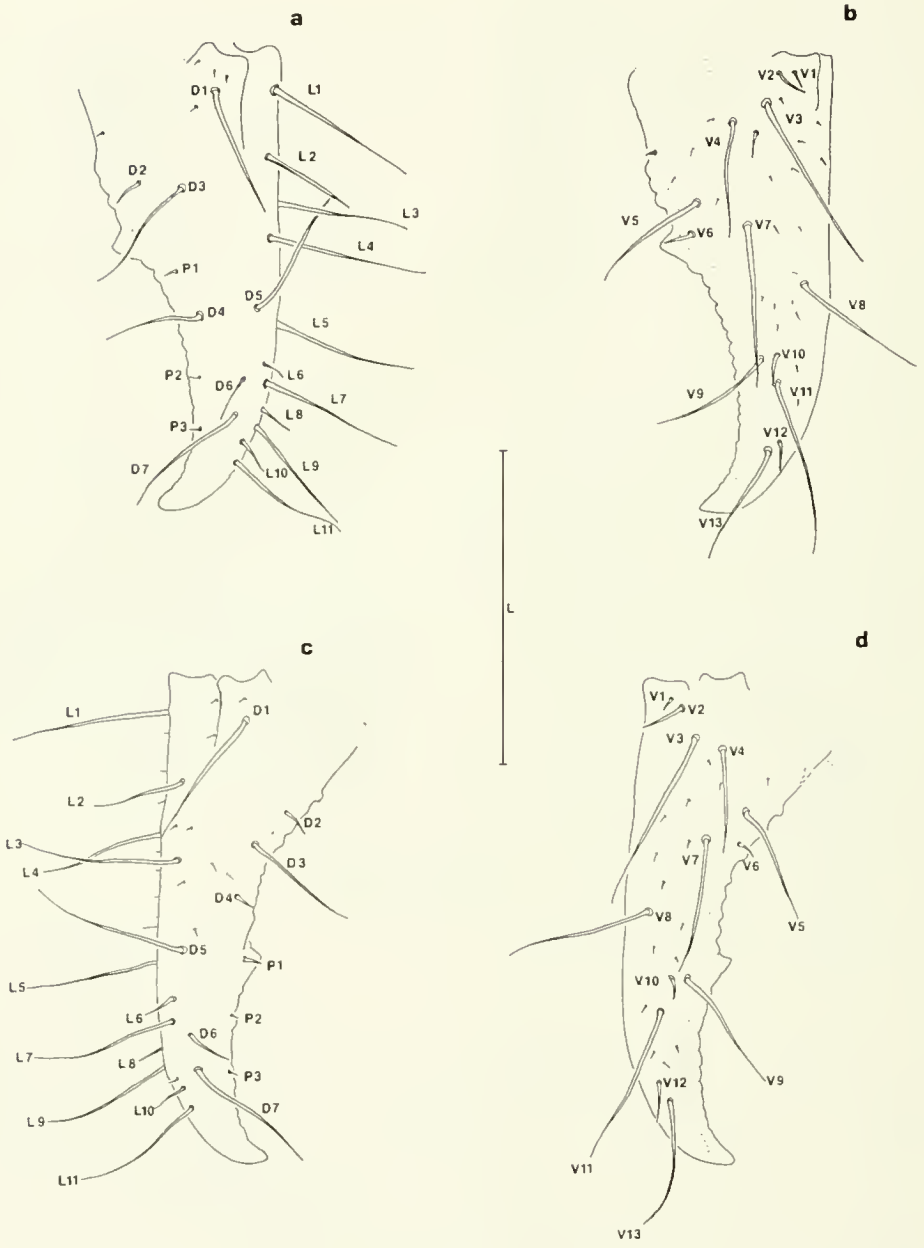

Fig. 2a–d. Chaetotaxy of female *Metajapyx heterocercus* cerci. a, Right dorsal view. b, Right ventral view. c, Left dorsal view. d, Left ventral view. L = 0.5 mm. Terms: D, dorsal setae; L, lateral setae; P, postdental margin stae; V, ventral setae.

of large setae progressively smaller on tergites III–VI and absent on tergite VII. Tergites III–V 5+5M, 2+2m, and scattered microsetae; tergite VI with M1 usually absent and posterolateral margins rounded, tergite VII with M1 always absent and posterolateral angles projected to the rear as blunt points (Fig. 1c). Tergite VIII 2+2M

Table 1. Mean number and range of laminal teeth in *Metajapyx heterocercus* and *Metajapyx magnifimbriatus*.

Lamina	Mean (Range)	
	M. heterocercus	*M. magnifimbriatus*
I	13 (11–14)	10 (10–11)
II	26 (24–29)	23 (21–24)
III	16 (14–18)	10 (9–11)
IV	17 (16–19)	14 (13–15)
V	14 (13–15)	13 (12–13)

and a few scattered microsetae; tergite IX 1+1M and a few scattered microsetae; plurae meeting in mid-ventral line, 2+2M and a few scattered microsetae. Tergite X with macrosetae A and B long, C absent, D minute or absent (Fig. 1c). Carinae distinct and nearly parallel; pygidium prominent and rounded.

Sternite I apotome 3+3m alternating with microsetae; sternite I 12+12M in four irregular transverse rows, scattered microsetae, and a group of two large posterolateral setae; antecedent setae 36+36 (29–39) and simple, in two irregular transverse rows, becoming sparse mesally; lateral subcoxal organs protruding from sternite, with 18+18 (12–23) glandular setae broad basally and gradually tapering apically, nearly as long as antecedent setae; 27+27 (21–38) hairlike sensory setae set in large setal sockets, about half as long as glandular setae (Fig. 1d); median glandular organ protruding, with 11 (8–14) contiguous disculi. Sternites II to VII 16+16M in transverse rows, 2+2m, and scattered microsetae; sternite VIII 7+7M and scattered microsetae.

Genitalia: Papillary area with groups of 11+11 (9–14) sensory pegs; anterior lobes with 4+4 (3–5) apical sensory pegs; posterior lobes with 4+4 (3–4) apical sensory pegs. Ventral carinae of segment X distinct with 10+10M and scattered microsetae.

Cerci: Right arm predental margin uniserrate with 4 (4–5) denticles, median tooth large and slightly rounded, postdental margin crenate; dorsal (D) surface with 7 setae, right lateral margin (L) with 11 setae, postdental margin (P) with 3 minute setae, and ventral (V) surface with 13 setae: D1 long, D2 short, D3–5 long, D6 short, and D7 long, L1–5 long, L6–11 alternating short with long; V1–2 short, V3–5 long, V6 short, V7–9 long, V10 short, V11–13 alternating long with short (Fig. 2a, b). Left arm predental margin biserrate with 9 (9–10) denticles in dorsal row and 9 (8–11) denticles in ventral row; median tooth large and slightly rounded, postdental margin crenate. Dorsal surface with the same number of setae as the right arm and L and P setal patterns same as right arm; D1–7 alternating long and short, V1 minute, V2 medium, V3–5 long, V6 short, V7–9 long, V10–13 alternating short and long (Fig. 2c, d).

Males.—Resembling females except tergite V with M1 sometimes absent, tergite VI with M1 usually absent and posterolateral margins usually projected back into rounded points (Fig. 1e), tergite X with A and C absent, B long, D minute or absent. Sternite I antecedent setae more numerous; slightly fewer glandular and sensory setae. Genital papillae conical, with 2+2 (1–3) apical sensory pegs and numerous short setae mesally and long setae distally; genital opening with numerous short marginal setae becoming progressively longer distally.

Cerci: Right arm predental margin uniserrate with four denticles, median tooth large, rounded, occasionally projected posteriorly, postdental margin crenate, slightly falcate (Fig. 1f). Chaetotaxy similar to female except L1 and V1 absent, and a short extra dorsal seta (D4'). Left arm similar to female except median tooth minute or absent, L1 absent, L6 long, L7 short; D4 minute, V1 and V6–8 absent.

Type material.—Holotype male and allotype female: Tennessee, Knox County, Cherokee Trail, 3.2 km south of the University of Tennessee (elevation ca. 650 meters), 24-X-1988; M. A. Muegge. Paratypes (4 males, 4 females): Same data as holotype and allotype. Habitat.—All specimens were

found 5–10 cm deep in moist gravelly clay soil or under rocks in a beech-maple forest. The holotype, allotype and two paratypes (1 male, 1 female) are deposited in the United States National Museum (USNM). The other paratypes (3 males, 3 females) are deposited in the Apterygote Section of the University of Tennessee Entomology Museum, Knoxville, TN. Etymology.—Greek *hetero* ("different"), Greek *cercus* ("tail"), which referes to the sexually dimorphic differences in the cerci.

Diagnosis.—Within the North American *Metajapyx* spp., female *M. heterocercus* appear to be most closely related to *M. steevesi*. Females of both species are nearly identical in form and chaetotaxy; however, *M. heterocercus* possess only simple antecedent setae, while *M. steevesi* usually possess at least a few fimbriate setae. Additionally, *M. heterocercus* differs by the chaetotaxy of tergite X (seta C absent and B bisects tergite X at ⅔ its length rather than ½ its length as in *M. steevesi*), and both cerci lack dorsal setae D1′ and usually D7′. Male *M. heterocercus* are taxonomically similar to *M. folsomi* Silvestri, yet *M. heterocercus* males are distinguished by possessing only a few simple antecedent setae that are generally uniform in size, tergite VI with the anteromedian pair of setae always present, and the median tooth of the left cercus minute or absent.

Metajapyx magnifimbriatus Muegge and Bernard

New Species

(Figs. 3a–f, 4a–e; Table 1)

Females.—Body length 9.2 (7.4–10.9) mm; all aspects of this species are similar to *M. heterocercus* unless otherwise noted.

Head: 30 antennal segments, terminal segment with 2 whorls each with 4 placoid sensilla; posterolateral proliferation of setae occurring on segments 13–17. Labial palpus with 10+10 setae; maxillary palpus with 18+18 (15–21) setae on terminal segment; all laminae of lacinia pectinate (Table 1).

Thorax: Mesonotum with 5+5M, 6+6m, and scattered microsetae (Fig. 3a).

Abdomen: Tergites VI and VII with M1 and AM always present, posterolateral margin of VI rectangular, VII projected back into sharp points, the latter occasionally falcate; tergite X setae A, B and C large, D minute or absent (Fig. 3b). Sternite I with 13+13M (12–14) in three transverse rows and scattered microsetae; antecedent setae 30+30 (29–32); subcoxal organs with 7+7 (4–10) glandular and 18+18 (15–23) sensory setae (Fig. 3c, d); median glandular organ protruding and with 11 (9–13) contiguous disculi; sternites II–VII with 17+17M in four transverse rows. Genital papillae with 8+8 (5–10) sensory pegs; anterior and posterior lobes with 3+3 sensory pegs.

Cerci: Right arm predental margin biserrate with 1:2, 2:2 or 2:3 denticles; median tooth medium and sharply pointed; postdental margin smooth to slightly crenulate and strongly falcate; chaetotaxy similar to *M. heterocercus* n. sp. except extra L4′ short, D1′ and D3′ long, and V7′ long (Fig. 4a, b). Left arm predental margin biserrate with 5 (4–5) dorsal toothlets and 7 (6–7) ventral denticles; median tooth small and sharply pointed; postdental margin smooth to slightly crenulate and sharply falcate; chaetotaxy similar to *M. heterocercus* n. sp. except extra L4′ short, D1′ long, D3′ long, and V7′ long (Fig. 4c, d).

Males.—Body length 9.4 (9.3–9.4) mm. Similar to female except: tergite VI with M1 occasionally absent and posterolateral margins usually projected back into sharp points; tergite VII with M1 always absent (Fig. 3e); sternite I with numerous fimbriate antecedent setae restricted to posterior third of sclerite becoming sparse mesally, and a few simple antecedent setae in an irregular transverse row anterior of subcoxal organs becoming sparse mesally (Fig. 3f). Genital papillae conical, with 2+2 apical sensory

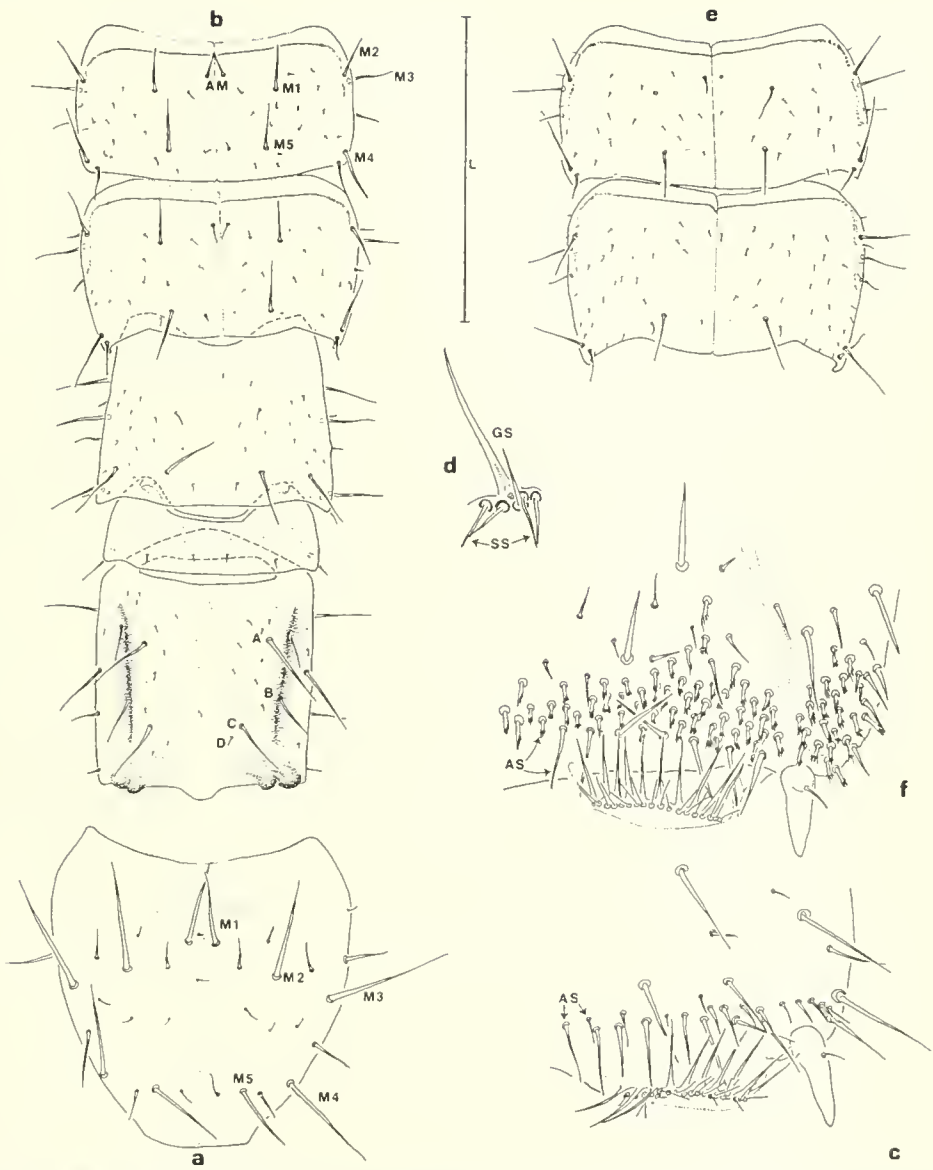

Fig. 3a–f. *Metajapyx magnifimbriatus*. a, Mesothorax, L = 0.5 mm. b, Tergites VI–X, L = 1.0 mm. c, 1st abdominal sternite of female, L = 0.25 mm. d, Sensory and glanular setae of lateral subcoxal organ, L = 0.1 mm. e, Tergites VI–VII of male, L = 1.0 mm. f, 1st abdominal sternite of male, L = 0.25 mm. Terms: AM, anteromedian pair of setae; M, macroseta; AS, antecedent setae; GS, glandular setae; SS, sensory setae.

pegs and numerous short setae mesally and long setae distally; genital opening with numerous minute marginal setae becoming longer distally.

Cerci: Right arm with predental margin biserrate with 1:2 or 1:3 denticles, chaetotaxy similar to female except L1 and L4′ absent, D2 and D4 minute, V1 and V2 absent, V3 and V5 medium, V7 and V7′ absent; left arm predental margin biserrate with

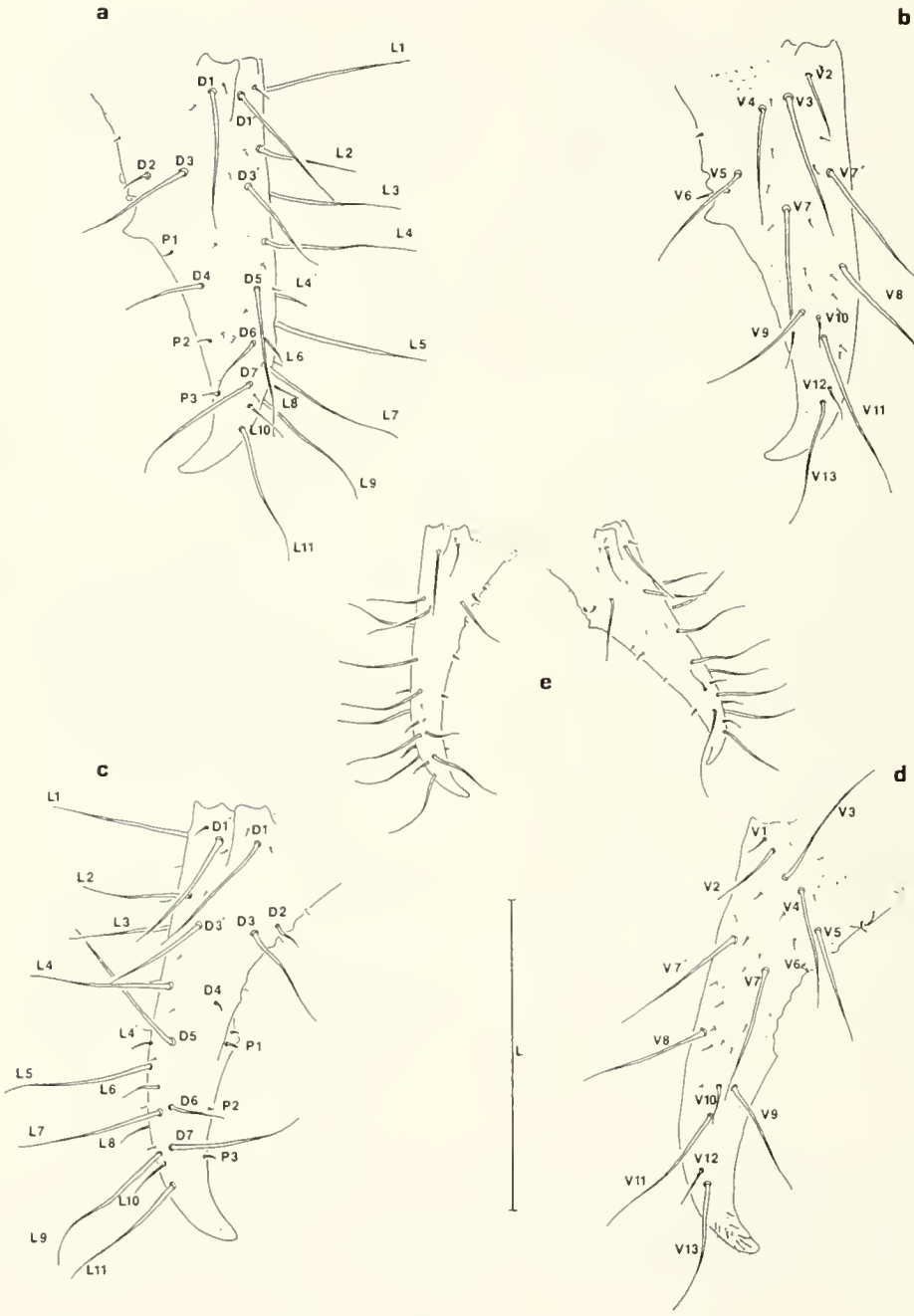

Fig. 4a–e. Chaetotaxy of male and female *Metajapyx magnifimbriatus*. a, Right dorsal view, L = 0.5 mm. b, Right ventral view, L = 0.5 mm. c, Left dorsal view, L = 0.5 mm. d, Left ventral view, L = 0.5 mm. e, Dorsal view of male cerci, L = 1.0 mm. Terms: D, dorsal setae; L, lateral setae; P, postdental margin setae; V, ventral setae.

5 (5–6) dorsal toothlets and 5 (4–6) ventral toothlets, median tooth minute and sharply pointed; chaetotaxy similar to female except L1 absent, D1 short, V1–2 absent, V3 medium, V5 short, and V6–7 absent (Fig. 4e).

Type material.—Holotype male and allotype female: Tennessee, Knox County, Cherokee Trail, 3.2 km south of the University of Tennessee (elevation ca. 650 meters), 24-X-1988; M. A. Muegge. Paratypes (2 males, 3 females): Same data as holotype and allotype. Habitat.—All specimens were found 15–30 cm deep in moist clay soil in a beech-maple forest. The holotype, allotype and two paratypes (1 male, 1 female) are deposited in the United States National Museum (USNM). The remaining paratypes (1 male, 2 females) are deposited in the Apterygote Section of the University of Tennessee Entomology Museum, Knoxville, TN. Etymology.—Latin *magni* ("great"), Latin *fimbriatus* ("fringed"), which refers to the numerous fringed antecedent setae of the male.

Diagnosis.—*Metajapyx magnifimbriatus* most closely resembles *M. multidens* (Cook) and *M. propinguus* (Silvestri), but may be easily distinguished from the latter two species by the following characters: 30 antennal segments, anteromedian pair of setae always present on tergites VI and VII, seta M1 always present on tergites VI and VII of female (M1 absent on VII and sometimes on VI for male), median tooth of cerci small and sharply pointed, and postdental margins of cerci smooth.

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SEASONAL ABUNDANCE AND HABITS OF THE BOXELDER BUG, *BOISEA TRIVITTATA* (SAY), IN AN URBAN ENVIRONMENT

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Abstract.—*Boisea trivittata* (Say) (Family Rhopalidae), the boxelder bug, is a common household pest in the United States. Large aggregations of adults and nymphs of this plant bug can form on the primary host tree, *Acer negundo* L., and other maples, or on buildings in urban environments. Overwintering boxelder bugs often seek harborage in protected areas around houses. The pest status of this insect is based primarily on the presence of large aggregations in the spring and the fall, and movement indoors where their excrement can stain fabric. Information on the biology and influence of substrate temperature on its activity was obtained from studies of laboratory and field populations in urban environments in Virginia. Adult boxelder bugs were present twice during the calendar year 1988. Overwintering adults were active from April to June, and first generation adults were present from August to October. In laboratory colonies, the number of days between mating and egg laying was 1–5, the mean number of eggs per mass was 9.5 (laboratory) and 9.9 (field), and the mean incubation period was 10 days. The range of survival was 1–22 days for males, and 1–20 days for females. Adult and nymphal boxelder bugs responded to temperature differences by aggregating on the warmest substrates available. Thoracic temperatures of adult boxelder bugs were significantly higher than ambient air, and the differences between substrate and thoracic temperatures ranged from 3.4 to 7.0°C.

Key Words: biology, mating, feeding, thoracic temperatures

Boisea trivittata (Say), the boxelder bug, is a scentless plant bug in the family Rhopalidae. It is a minor pest of some fruit crops, and a widely distributed, common household pest in the United States (Wheeler 1982). Boxelder bugs are usually found near their primary host, the boxelder tree, *Acer negundo* L. However, feeding is not restricted to this species of maple. *B. trivittata* has been found feeding on other trees, including *A. saccharinum* (L.), *Quercus* spp., and *Ailanthus altissima* (Mill.) (McDaniel 1933, Smith and Shepherd 1937, Wheeler 1982).

Large aggregations of adults and nymphs can form on houses during spring and fall and cause concern among homeowners. Overwintering boxelder bugs move into houses through open windows and doors, and cracks and crevices around windows, doors, and eaves in the fall. When indoors, adults can stain fabric with their excrement (Davis and Joos 1982). Taub (1970) reported severe asthmatic reactions during fall migrations of boxelder bugs into homes. The pest status of *B. trivittata* was reported by Swenk (1929), Ascerno (1981), and Pinkston (1988).

Early studies focused on the geographic distribution, taxonomy, morphology, and development of *B. trivittata* (Howard 1898, Smith and Shepherd 1937, Knowlton 1944, Tinker 1952). The objectives of the research

reported here were to elucidate seasonal abundance, life cycle data, microhabitat temperature preferences, and boxelder bug activity in response to temperature in an urban environment.

Materials and Methods

Seasonal abundance.—Field populations of boxelder bugs were sampled from April to December, 1988, at three houses, three apartment buildings, and one utility building in Blacksburg, Virginia. These structures were inspected three times per month for boxelder bugs. The base of the foundation walls on the south and west exposures were partitioned into one meter squares with spray paint. The wall, ground, and vegetation located within sample squares were examined, and all adult and nymphal boxelder bugs within the square were recorded. The total number of insects in each square were summed over all squares per site.

At one apartment building (site F) three boxelder trees located approximately 10 m from the building were sampled for adults and nymphs with a plastic container and hand brush. The opening of the container contained a funnel and was held at the base of the tree. Boxelder bugs were lightly brushed from the bark into the container. After sampling, the containers were returned to the laboratory and the bugs were sexed, counted, and later returned to the trees and released.

The sex ratio of overwintering adults was determined from boxelder bug populations at four building sites. Four samples were taken each week for a five-week period from September and December, 1988. Samples of soil and leaf litter were removed from the southwest exposure of the building and taken to the laboratory where boxelder bugs were removed, sexed and counted.

Biological information.—Laboratory colonies were initiated with adults obtained from field populations in Blacksburg, Virginia in spring, 1988. Rearing methods were similar to those reported by Smith and Shepherd (1937). Thirty-eight females and 30 males were maintained in the laboratory for life history studies. Pairs were maintained in 3.8 liter glass jars and provided with fresh boxelder leaves and water. Water bottles and leaf material were replaced daily. Mortality was recorded daily and dead individuals were removed and replaced. Egg masses were transferred from jars to petri dishes (100 × 15 mm). After hatch, first instar nymphs were transferred to plastic cups (9.5 × 5.5 × 8 cm) and supplied with small boxelder leaves. Cheesecloth was used to retain nymphs and adults in the containers. Rearing conditions were 20–22°C, 58–62% RH, and 12:12 h photoperiod.

Temperature selection.—Visual observations were conducted on the activity of adults and nymphs in response to sunlight. The movement of second-generation boxelder bugs on the trunks of three boxelder trees was recorded several times during the day in September.

Temperatures from substrates on three houses (A, B, C) in Blacksburg were recorded from October 21 to November 15. The substrates included white-painted, aluminum siding, concrete, brick, and colored canvas. The houses were selected on the basis of existing infestations of boxelder bugs. An insulated thermistor probe attached to a micrologger (Campbell CR21 Micrologger) was used to measure temperatures in the microhabitats sampled. The styrofoam-insulated (2 layers) thermistor probe was attached to the substrates for 6 min. Ambient air temperature was measured by placing the probe in the air and recording for 15 min. The micrologger was programmed to record maximum, minimum, and average temperatures every 3 min. Records were maintained for the time, Julian day, and microhabitat where the probe recorded temperature. Data were loaded onto a cassette recorder and transferred to an IBM mainframe computer program for analysis.

Internal thoracic temperatures of 156 adult boxelder bugs at sites A, B, and C were

taken with a 0.03 cm chrome-alumel (Omega) thermocouple insulated with Tygon tubing. The thorax was held with rubber gloves and forceps, and the thermocouple inserted posteroventrally between the second and third coxae. Because of the large size of the thermocouple, a time-constant of fifteen seconds was used to record temperatures. The specific microhabitat where the insects were found was also recorded.

Data were analyzed using the SAS-GLM procedures (SAS Institute Inc. 1985); the Student-Newman-Keuls Range test was used to separate means.

Results and Discussion

Seasonal abundance.—Adult boxelder bugs are present twice during the calendar year. The surviving overwintering adults are active in the spring. The first generation adults produced that year are present in late summer and fall, and form the overwintering population. Wollerman (1965) reported two generations of the boxelder bug in the South and one in the North. Smith and Shepherd (1937) reported two generations of boxelder bugs in Kansas.

Overwintering generation.—Adults were found primarily in leaf litter, on bark around *A. negundo* and *A. saccharinum* trees, and in mulch on southern exposures of residences. During April, some adults observed at overwintering sites became active. Mating activity was observed from March 11 to June 15 on the outside walls of residences, at the base of *A. negundo* and *A. saccharinum* trees, and on low vegetation around residences.

Females laid eggs predominantly on the surface of buildings in April and May. Egg deposition sites appeared to shift to low vegetation from June to August. First-generation eggs were first observed on April 14, and nymphs appeared during the second week of May. Egg deposition by first-generation adults ceased the last week in June. The mean number of eggs per mass counted in the field was 9.9 (n = 123.0; SD = 4.3; range = 2–21). The mean percentage egg hatch was 84.4%. The number of nymphs increased during the last week of June, and numbers peaked during the first week of July. This increase was followed by a low number of nymphs observed from the end of July through August. The number of adult boxelder bugs at all sites remained low until mid-June. There was a gradual increase in the number of adults observed from mid-June to the end of July.

Adults were observed mating and feeding on female boxelder trees in mid-July. No mating was observed on low vegetation during July or August. A general decrease in the adult population was observed during August. Tinker (1951) reported adults feeding and mating on female boxelder trees in August and September. The results from this study indicate that during late summer first-generation adults move from buildings to host trees and ground sites.

First generation.—An increase in the number of first-generation nymphs occurred during late August to September (Fig. 2). A decline in the nymphal population occurred in October, and only small numbers of nymphs were observed from October through December. A decreased number of nymphs was followed by an increase in the number of adults observed on the surfaces of buildings in mid-October. Movement of adults to buildings at all of the sites occurred at this time. Tinker (1951) reported an abundance of adults in August and September on female boxelder trees in Minnesota, which coincided with the development and maturity of the *A. negundo* ovules. Smith and Shepherd (1937) reported that boxelder bugs sought shelter in early October, and movement out of hibernation began in late March in Kansas. Time of dispersal to search for feeding or overwintering sites may vary with geographic location (Wollerman 1965).

The sex ratio of second-generation adults was approximately 1:1. The ratio reported here contradicts the ratio (2:1, female : male)

reported by Smith and Shepherd (1937). The method of sampling adults could account for the disparity in the ratio reported by Smith and Shepherd (1937) and that reported here.

Life cycle

Laboratory colony.—Mating did not occur immediately after adults were paired in rearing jars. Mating behavior was not observed until several days after males and females were placed in the jars. When two males were placed with one female there was often aggression between the males when both attempted to copulate with the female. Several observations were made of males that mounted females on the posterodorsal side and extended their beak between the elytra of the female. Of the 38 females observed, 16 did not lay eggs. The number of days between mating and egg laying ranged from 1 to 5 (n = 22).

In the laboratory the mean number of eggs per mass was 9.5 (n = 33, SD = 7.7). Smith and Shepherd (1937) reported an average of 10 eggs per mass. The mean incubation period calculated from all eggs for all batches was 10 days. The incubation period was 12 and 13 days for eggs from females that laid 2 and 3 batches, respectively. Smith and Shepherd (1937) reported a range between 11 and 19 days and a mean of 13 days for boxelder bug oviposition period. Egg batches were laid in various size groups. Newly laid eggs were light orange, but turned dark red before hatching. Forty-one percent of the females laid no eggs, 43.6% laid 1 batch, 10.3% laid 2 batches, and 5.1% laid 3 egg batches.

The mean survival of adults in the laboratory was 7.6 days (n = 37; SE = 5.6) for the females and 8.8 days for males (n = 29; SE = 6.27). The range of survival was 1–22 days for males and 1–20 days for females. The average number of days death occurred after eggs were laid was 4.3 days.

Microhabitat temperature selection

Substrates.—Observations of second-generation adults and nymphs on three trees indicated that they oriented primarily toward the side of the trees that received the most sunlight. In the morning a large number of bugs gathered on the eastern-exposed portion of the trunk, and in late afternoon more boxelder bugs were seen on the western exposure. At approximately 9:00 am, an increase in adult and nymphal activity was observed, including movement to the ground at the base of the trees. They may have responded to a change in the incident angle of the sun and temperature. Tinker (1951) reported a preference for sunny exposures of *A. negundo*, but aggregations of bugs dispersed when the area became shaded.

The mean temperatures recorded on southern-exposed substrates of three houses (A–C) are shown in Table 1. The number of boxelder bugs was greatest on substrates that had higher temperatures. At house A the mean temperature (26.5°C) recorded on the white-painted aluminum siding was not significantly different ($P > 0.05$) from the mean temperature (24.3°C) recorded at the concrete foundation. Although there was only a 2.2°C difference in temperatures recorded from the two substrates, there were 113 boxelder bugs on the siding, and 23 boxelder bugs on the concrete foundation.

At house B a mean temperature of 25.2°C was recorded on a window shutter, and this temperature was significantly different ($P < 0.001$) from the 17.9°C recorded behind a rain gutter on that house. Apparently, boxelder bugs at this site responded to the 7.3°C temperature difference by aggregating on the warmer substrate (240 on the window shutter vs. 8 at the rain gutter). Of the approximately 500 boxelder bugs collected at house C, 56 boxelder bugs were recorded on the cement foundation, which had a temperature of 17.1°C. However, 240 boxelder bugs were collected from a piece of blue canvas

Table 1. Microhabitat mean temperatures for boxelder bugs at three sites.

Site	Microhabitat	Temp (C)*	No. Bugs
A	white aluminum siding	26.5a	113
	white alum. siding (east)	15.4b	10
	white alum. siding (north)	10.9c	0
	white alum. siding (west)	27.4a	27
	concrete foundation	24.3a	23
B	window shutter	25.2a	240
	brick	24.7a	140
	rain gutter	17.9b	8
C	blue canvas	24.9a	240
	white aluminum siding	20.2b	121
	concrete	17.1b	56

* Range of 2–5 separate temperature recordings.
Means in each column followed by the same letter are not significantly different (Student-Newman-Keuls multiple range test; $P > 0.05$).

(24.9°C) on the house. Tinker (1952) reported that as little as a 1.0°C to 3.3°C difference between substrates resulted in boxelder bug aggregations on surfaces with the higher temperature.

Insect.—Boxelder bug thoracic temperatures were significantly higher than the ambient temperature; the differences ranged from 3.2 to 3.5°C at three locations ($P < 0.001$) (Table 2). The substrate surface temperatures were always significantly greater than the ambient and thoracic temperatures in the four locations sampled ($P < 0.001$). Differences between substrates and thoracic temperatures ranged between 3.4 and 7.0. The thoracic temperatures may more closely match the temperature of the air immediately above the substrate. Solar radiation heats the boundary layer of air above sunlighted substrates. The temperature differences between substrates, boundary layer air, and ambient may be several degrees (Heath and Wilkin 1970). Heath and Wilkin (1970) reported the thoracic temperature of a desert cicada to be closer to the temperature of the boundary layer air than to that of the substrate or ambient air.

Conclusions

The boxelder bug is a unique pest in the urban environment. Unlike a year-round indoor pest, such as the German cockroach, the boxelder bug is a pest only during spring and fall, but affects urban residents both indoors and outdoors. The apparent preference of the adults and nymphs for warm or heat-retentive surfaces, and the large populations twice each year make this insect an important urban pest. Its pest status is based on the numbers found aggregating in

Table 2. Mean comparisons of thoracic, substrate and ambient air temperatures of boxelder bugs at four locations.

Subject	Temperatures (n) and Locations			
	A	B	C	D
Substrate	28.7a (38)	28.5a (6)	20.3a (11)	20.8a (8)
Thorax	24.9b (8)	21.5b (27)	16.9b (42)	19.8a (17)
Ambient air	21.4c (14)	21.9b (20)	13.7c (10)	16.3b (17)

Means in each column followed by the same letter are not significantly different (Student-Newman-Keuls multiple range test; $P > 0.05$).

and around houses, and its pest importance is indicated by the amount of money urban residents spend on control (Yoder and Robinson 1988).

Nonchemical control strategies for this insect are limited. Smith and Shepherd (1937) reported that no parasites emerged from 452 eggs they observed during rearing. Smith and Shepherd (1937) reported parasitic flagellates in the intestinal tract of *B. trivittata,* but did not appear to cause mortality. Removal of the host tree may be effective (Davis and Joos 1982), and sealing crevices in structures may prevent boxelder bugs from moving indoors. However, Smith and Shepherd (1937) and Wheeler (1982) reported that *B. trivittata* can feed on a variety of ornamental trees and plants. Chemical control of this insect presents several problems. Because this insect is a problem to homeowners primarily during spring and fall, chemical controls are usually initiated after large numbers of bugs aggregate around houses. Photodegradation and volatilization of commonly used insecticides can occur because they are applied to sun-exposed and heat-retaining surfaces. These surfaces are attractive to the insects, but limit insecticide effectiveness. It would be more effective to time and direct chemical applications to the eggs and early instars of the first generation.

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EGG DISPERSION IN TWO SPECIES OF PRAYING MANTIDS (MANTODEA: MANTIDAE)

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Abstract.—*Tenodera sinensis* (Saussure) and *Mantis religiosa* (Linnaeus) are univoltine generalist predators which produce eggs at the end of the growing season. Oothecae of both species exhibit a markedly contagious dispersion in old fields in northern Delaware. In view of the large number of eggs contained in each ootheca, the propensity for synchronous egg hatch for each species, and severe food limitation during emergence early in the spring, such clumping is surprising since it places newly-hatched nymphs at a greater risk of cannibalism and competition from their cohort than if they were more uniformly distributed in space. Possible explanations for such clumping are discussed.

Key Words: Mantodea, Mantidae, *Tenodera sinensis, Mantis regligiosa,* dispersion, predators

The praying mantids *Tenodera sinensis* (Saussure) and *Mantis religiosa* (Linnaeus) are generalist predators which commonly occur in old fields in northern Delaware. Both species produce oothecae which may contain several hundred eggs each, and although eggs of *T. sinensis* generally hatch before those of *M. religiosa,* there is considerable intraspecific synchrony (Hurd and Eisenberg 1988a). Egg hatch occurs early in the spring, when there is normally a shortage of suitable prey (Hurd and Eisenberg 1988b, Rathet and Hurd 1983). We have shown that early instar nymphs of *T. sinensis* show a strong tendency to disperse (Hurd and Eisenberg 1984). We also know that first stadia of both species will resort to cannibalism when alternative food is absent (Hurd and Eisenberg 1984, unpublished laboratory observations). Given the above information, it would seem reasonable to expect that for both of these species, oothecae should not be clumped. Females which deposit an egg mass close to another egg mass would seem to be placing their young at a disadvantage in terms of increasing the potential for both intraspecific competition and cannibalism (Hurd 1988). We therefore decided to determine the spatial dispersion of oothecae of these two species in local old fields.

Materials and Methods

Three different old fields in the vicinity of the University of Delaware campus in Newark, Delaware, were used for the collection of data. One was a late successional goldenrod field (field #1); the other two were sites AG (field #2) and CHRY (field #3) referred to by Hurd and Eisenberg (1988a, b). All three had been examined for several years and were known to harbor persistent populations of mantids.

The portion of each field which constituted mantid habitat was staked out. Areas thereby delineated were searched for oothecae and the location of each was marked with a 1.0 m wooden dowel. After searching

Table 1. Results of oothecae censuses and nearest neighbor analyses for three fields. Ts = *Tenodera sinensis*, Mr = *Mantis religiosa*. R = ratio of observed mean distance to nearest neighbor to expected mean distance to nearest neighbor. *P* values are based on values of C (Clark and Evans 1954).

Site	Site Area (m^2)	Species	Number of Oothecae	R	*P* Value
Field #1	1200	Ts	119	0.76	<.01
Field #2	700	Ts	59	0.48	<.01
Field #3	1000	Mr	101	0.76	<.01

was completed the distance of each ootheca to two reference stakes was measured to the nearest cm using a pair of measuring tapes. In the laboratory this information was used to locate each ootheca on a scale map of each area, and dispersion was determined by nearest neighbor measurements (Clark and Evans 1954).

Results and Discussion

While we encountered both species of mantids in each of our collections, only a single species was numerous enough in each field to permit dispersion analysis. In fields #1 and #2 the dominant mantid was *T. sinensis*, and oothecae were mainly located on dead, upright plant stems from 0.3 to 1.0 m above the ground. In field #3 the dominant mantid was *M. religiosa*, the oothecae of which were mainly found in the dense, overlapping grasses which comprised ground cover in these fields. In all three fields the nearest neighbor analysis shows a highly significant departure from random expectation (Table 1). An R value of 1.0 is expected if the observed pattern is random. Our R values of 0.48 to 0.76 indicate that the distributions of oothecae of both *M. religiosa* and *T. sinensis* are very contagious; both of these mantid species show a strong tendency to deposit egg masses in close proximity to other conspecific oothecae.

The average field-collected ootheca of *T. sinensis* weighs approximately 1.9 g and releases 240 nymphs (Eisenberg and Hurd 1977). Mean weight of *M. religiosa* oothecae collected from our study fields was 1.07 g, emergence ranging from 30 to 370 nymphs with a mean of 156. Both species display considerable synchrony of emergence in the field. Thus, in addition to the high local density produced by the hatching of a single ootheca, the close proximity of additional oothecae can result in even higher densities. In field #1, 29.4% of oothecae were within the same 1 m^2 area as another ootheca and 48.7% were within the same 2 m^2 area. In field #2, 61.0% of oothecae were within the same 1 m^2 area as another ootheca and 71.2% were within the same 2 m^2 area. For field #3 the values were 19.8% and 30.7% respectively. Thus at emergence time, local densities of nymphs easily could reach or exceed 300 to 400 nymphs per m^2.

How can we explain the contagious nature of the oothecae pattern? During the late summer and fall of each year, *T. sinensis* often can be found on inflorescences of late-flowering plants such as goldenrods and asters, which attract prey in the form of flower-foraging insects including pollinators. This represents an important source of nutrition for females while they are undergoing oogenesis; females so positioned produce more eggs than those which are on plants not in flower (Hurd 1989). Females generally do not move around once they mature (Bartley 1982), so that a female's position on a specific plant (in flower or not) may be a matter of chance rather than choice. However, the clonal nature of these flowering plants produces clumps of the most nutritionally rewarding oviposition sites, which could in turn explain contagion among oothecae. An alternative explanation, that females oviposit more than once, is less likely because normally there is not sufficient time between first oviposition and killing frost for this species to generate a second ootheca in our geographical region in the face of rapidly decreasing food levels at the end of the growing season (Eisenberg, Hurd and Bartley 1981).

Mantis religiosa exhibits a very different set of behaviors in regard to its foraging activities. This species tends to forage closer to the ground than *T. sinensis* (Rathet and Hurd 1983), and thus is less likely to be found on the taller flowering plants. While this species also will deposit its oothecae on upright stems, apparently it prefers grasses located much closer to the ground. These grasses do not have flowers to attract supplemental food, and constitute a much denser, less patchy vegetational layer than goldenrod. We do not know if this species faces the same degree of food limitation as *T. sinensis* at the end of the growing season, so that it is possible that multiple oviposition is responsible for the contagious distribution of *M. religiosa* oothecae. However, this still leaves open the question as to why a female would crowd her own offspring, an apparently maladaptive trait.

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NOTE

First Distributional Records of *Cimexopsis nyctalis* List (Hemiptera: Cimicidae) in Connecticut

Cimexopsis nyctalis List is restricted to the eastern United States where it inhabits nests of the chimney swift, *Chaetura pelagica* (Linnaeus) (Usinger 1966. Monograph of Cimicidae (Hemiptera–Heteroptera), Vol. 7. Thomas Say Foundation. Entomological Society of America, Baltimore, Maryland. 585 pp.). This insect is known to occur in 16 states (Lee 1955. Bull. Brooklyn Entomol. Soc. 50: 51–52.), (Usinger, ibid.).

Three unreported records of *C. nyctalis* from Connecticut are: New Haven County, Branford, 30 July 1942 (1 specimen); Litchfield County, Thomaston, 1 August 1942 (3 specimens from a chimney); and Tolland County, Manchester, 22 August 1988 (1 specimen). The specimens from Branford and Thomaston, housed in the Connecticut Agricultural Experiment Station insect collection, were previously identified incorrectly as *Oeciacus vicarius* Horvath. The specimen from Manchester was collected inside a home where birds were nesting in the chimney during 1987 and 1988. The person who collected *C. nyctalis* in Manchester reported that she was bitten by similar insects. *C. nyctalis*, whose only recorded host is *C. pelagica*, is not known to bite humans. However, it is not uncommon for other species of bird bugs to do so on occasion. For example, Harwood and James (1979. Entomology in Human and Animal Health. Macmillan Publishing Co., Inc., New York) reported that the swallow bug, *O. vicarius* Horvath, and the Mexican chicken bug, *Haematosiphon inodorus* (Duges), bite humans infrequently. All specimens are deposited in the insect collection of the Connecticut Agricultural Experiment Station. No specimens were found in the insect collections of the University of Connecticut (Storrs, CT) and Peabody Museum, Yale University (New Haven, CT).

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NOTE

Liliacina diversipes (Kirby) (Hymenoptera: Tenthredinidae), a Sawfly Genus and Species New to the United States

Dr. Henri Goulet, Biosystematics Research Centre, Agriculture Canada, Ottawa, discovered two specimens of a neotropical-like sawfly collected by Malaise trap in Alachua Co., Florida. These specimens are here identified as *Liliacina diversipes* (Kirby) (Selandriinae), a species native to Mexico and Central America. The species is apparently established in Florida and undoubtedly the result of an accidental introduction. Both the genus and species are new to the United States. The host is not known, though most nearctic Selandriinae feed on various ferns and sedges.

Liliacina was described by Malaise (1942, Ent. Tidskr. 63: 94, 99–100; type species—*Liliacina carinifrons* Malaise), includes about 8 species, and occurs from Mexico to southeastern Brazil and northern Argentina. It is distinguished from other North American Selandriinae genera (revision by Smith, D. R. 1969, U.S. Dept. Agr., Tech. Bull. 1398, 48 pp.) by the clypeus shallowly, semicircularly emarginate; tarsal claw with long inner tooth but without basal lobe; epicnemium (previously termed prepectus) elongate, on same level as mesepisternum and separated from mesepisternum by suture; genal carina absent; anal crossvein of forewing absent; width of malar space about half diameter of an ocellus; and antennal pedicel slightly longer than wide.

Liliacina diversipes (Kirby 1882, List Hym. Brit. Mus., vol. 1, pp. 189–190, pl. 8, fig. 22; described as *Selandria diversipes*; transferred to *Liliacina* by Malaise 1942) was described from "Mexico, Orizaba." I have seen specimens from Mexico (Jalisco, Veracruz), Guatemala, El Salvador, Costa Rica, Panama, and Colombia. The species is 8.0–9.0 mm in length, and coloration distinguishes it from all other North American Selandriinae: Head and antenna black with scape and pedicel brownish and clypeus, labrum, and base of mandible white; apex of mandible reddish; palpi blackish though basal segments and labium whitish. Thorax whitish (pale areas probably lilac-colored when alive) with cervical sclerites, mesosternum (except medial stripe), lower half of mesepimeron, most of mesoprescutum, most of mesoscutellum, and metathorax (except upper portion of metapleuron) black; mesonotal lateral lobes whitish to orange. Abdomen black, narrow posterior margin of segments whitish. Legs white with extreme base of hindcoxa, apical half of fore- and midtibiae, apical third of hindtibia, and all tarsi black. Wings blackish; veins and stigma black. The pale areas of the thorax are bright lilac in some neotropical specimens examined, but this turns to a sordid whitish in some preserved specimens, especially those collected in alcohol.

The collection data are as follows: USA: Fl., Alachua Co., Gainesville, AEI [American Entomological Institute], B.R.C. [Biosystematics Research Centre] Hym. Team. The two females were collected on 3–17-VII-1987 and 10–31-VIII-1987.

David R. Smith, *Systematic Entomology Laboratory, PSI, ARS, U.S. Department of Agriculture, % National Museum of Natural History, NHB 168, Washington, D.C. 20560.*

PROC. ENTOMOL. SOC. WASH.
92(4), 1990, pp. 813

NOTE

Coptotermes crassus Ping Preoccupied by *C. crassus* Snyder Renamed *C. pingi* (Isoptera: Rhinotermitidae)

In the course of compiling a list of species of the Isoptera of the world, an unusual taxonomic mistake was discovered. A newly described termite from China of the genus *Coptotermes* was given the specific name *crassus* (Ping, Z. 1985. Eight new species of the genus *Coptotermes* and *Reticulitermes* from Guangdong Province, China. Entomotaxonomia 7(4): 317–328 (pp. 319–320, 327, fig. 3A–E)). Unfortunately, the name *Coptotermes crassus* is already occupied by a Neotropical species (Snyder 1922. Proc. U.S. Natl. Mus. 61: 1–32 (pp. 21–22, fig. 6)). Thus according to Article 60(a) of ICZN (Ride et al. 1985. Internatl. Code Zool. Nomen. 3rd ed., Univ. Cal. Press, Berkeley, 338 pp.) *Coptotermes crassus* Ping is a junior homonym and must be rejected. Since Ping placed *crassus* directly in the genus *Coptotermes*, i.e. this combination did not arise from revision, *C. crassus* Ping 1985 is known as an objectively invalid primary junior homonym. Barring the possible availability of other names, a replacement name (*nomen novum*) with its own author and date needs to be designated (Article 60(c)). There is no reason to suspect that *C. crassus* Snyder and *C. crassus* Ping are synonymous—neither on the basis of morphology nor on the basis of geographic distribution (Araujo 1977. Catalogo dos Isoptera do Nova Mundo. Academia Brasileira de Ciencias, Rio de Janeiro). The only possible available name for a *Coptotermes* from that area is *hongkonensis* Oshima (Oshima 1914. Annot. Zool. Jap. 8: 553–585 (pp. 559–560, pl. IX, fig. 5)) which was sunken into synonymy with *Coptotermes formosanus* Shiraki. However, the ranges of all the measurements given by Oshima for *hongkonensis* are outside of those given for *crassus* Ping. Other details of the descriptions and illustrations also do not match. The right soldier mandible of *crassus* Ping is strongly curved toward the tip while it is relatively straight, "saber-shaped," in the photograph of *hongkonensis*. The soldier gula is strongly contracted in the middle in *crassus* Ping while only "slightly contracted at middle" in *hongkonensis*. The labrum reaches well beyond the middle of the soldier mandibles in *crassus* Ping while Oshima states that in *hongkonensis* it is "scarcely reaching the middle of the mandibles." Therefore, since *C. crassus* Ping cannot be referred to *C. hongkonensis*, and since there are no other available names from that area I propose the new name: *Coptotermes pingi* Myles Nomen Novum = *Coptotermes crassus* Ping 1985.

It is appropriate to rename this species after Dr. Ping Zhengming in recognition of his substantial contributions to termite taxonomy in China.

Timothy G. Myles, *Research Associate, Department of Entomology, University of Arizona, Tucson, Arizona 85721.*

PROC. ENTOMOL. SOC. WASH.
92(4), 1990, pp. 814–815

Book Review

Bird Blow Flies (Protocalliphora) *in North America (Diptera: Calliphoridae) with Notes on the Palearctic Species.* C. W. Sabrosky, G. F. Bennett, and T. L. Whitworth. Smithsonian Institution Press, Washington, D.C., and London [x and] 312 pp., paperbound. 1989. $16.95. Order from: Smithsonian Institution Press, Dept. 900, Blue Ridge Summit, PA 17294 (add $2.25 for postage and handling).

Maggots of bird blow flies are obligatory blood feeders that live exclusively at the expense of nestling birds. Adult flies are not commonly seen or collected in flight. They are fairly large, 9–12 mm long, and most commonly dark metallic blue, although the females of some species are bronze or copper. *Protocalliphora* is a Holarctic genus; 26 species, 15 of them new to science, are now known to occur in North America, and the ranges of two species extend into Europe.

This work is a fine, comprehensive systematic study of the genus *Protocalliphora* and its Nearctic species. It is based on Sabrosky's long-term taxonomic studies, Bennett's and Whitworth's individual field investigations, and Bennett's anatomical studies of the immature stages, all collated here by Sabrosky. The book is divided into two parts. The first, 43 pages long, is a general exposition of the taxonomy, geographical distribution, life history, and ecology, with tips on study and control. The remainder of the book, titled the taxonomic section, covers generic taxonomy, anatomy of all stages supported by illustrations for adults and a glossary for immature stages, keys to species, and individual treatment of all species. The descriptions are followed by a list of the avian hosts of Nearctic *Protocalliphora*, annotated references, an index to bird hosts and one to *Protocalliphora* and miscellaneous names, plates of illustrations and distribution maps.

The first part, at least, should fascinate anyone with passing interest in bird life, and the whole book, even the "legal" aspects of taxonomy, is engagingly written. The authors point out that these insects are barely or not at all mentioned in bird books or textbooks on parasitology, even though the maggots are common and numerous in bird nests. Publication of this book should make researchers much more aware that these insects exist.

The species treatments are helpfully broken down into short, topical subsections. The bibliography is annotated, a measure of the care taken with the book. I like the combined key to males, females, and puparia, which the authors show is the best way to determine *Protocalliphora* species. Anyone doing serious work with these flies will have both sexes and all stages available. Additional keys to each sex alone and to third instars are here also, but are less useful: the few easy-to-separate species are keyed first, but as the key goes along differences become finer so that a person will be less sure of what is in hand.

The authors wring their hands a little too much for my taste about what they consider to be drawbacks of the study: that it is not definitive (preface), that the distribution of many species is spottily known and that few areas have been studied thoroughly (p. 3), that any general statements should be qualified "as far as known" (p. 16), that the entire life history has not been followed for any species (p. 20), and that speculation on phylogeny seems premature (p. 37). These are all true statements that could have been rephrased in a positive manner, and deservedly so for all the painstaking study and time that the authors have invested in this project. This book will still be the authoritative work on *Protocalliphora* for a long time to come.

Non-entomologists who need this book and have no mental picture of a calliphorid may be put off by the lack of illustrations

of an entire adult and larva. An illustration of a larva to show the characteristic fringe of long setae around the head segment would also have served to distinguish *Protocalliphora* from other maggots likely to be found in bird nests. Reference is made to a drawing of anterior parts of a larva in another work, but that book may not be readily available to all. Further, books for general readers shouldn't have a lengthy quote in a foreign language (p. 9) or use dipterists' jargon or technical terms (eclose, myiasis, puparium) without a glossary. Authors' lapses are few and minor, among which are the lack of an authorial reference for a future publication on details of life history and biology (top p. 24) and five misspelled place names.

A publisher's note on the verso of the title page advises that, "For reasons of speed and economy, this book is prepared from camera-ready copy prepared electronically by the authors, who assume full responsibility for the contents and form." The claim notwithstanding, I cannot fault the authors for the Press's lack of oversight on this book. It resulted in weak major headings, the awkward blank bottom third of p. 56, the need of additional lines and leaders in some key couplets, a clumsy insert in the key on p. 86 (couplet 9a), the indexes appearing before the end of the book, and the fact that there are two indexes (one for bird names, one to other names) where one index would have served better. The indexes inconveniently precede the 33 pages of plates and maps, which themselves are not indexed. Further, the figures on pages 276–298 are reduced too much and are less effective for it; they could have been shown twice as large if they had been reconfigured. It is understandable that a press would want to keep costs low, but it must still attract authors and stand behind its product.

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Book Review

Insect Flight. 1989. G. J. Goldsworthy and C. H. Wheeler (eds.) C.R.C. Press, Inc., Boca Raton, Florida.

Few insect behaviors rival the significance of flight. Considering all the invertebrates, insects are the only ones to explore and succeed in using flight as a mechanism to locate new breeding sites, find food, escape predators, avoid unfavorable environmental conditions, and search for potential mates. *Insect Flight* is a literary tribute to this singular behavior that has culminated in the success of insects. This recent look at flight is an attempt to provide its readers with an up-to-date synthesis of the diverse topics that encompass this most important insect adaptation. The editors Graham Goldsworthy and Colin Wheeler should be complimented for providing such an impressive group of contributing authors (i.e. 18 in all). The coverage is broad and ranges in scope from the mechanisms and aerodynamics of flight (Chapt. 1) to the importance of understanding flight in the context of developing better control strategies (Chapt. 15). The chapters are well written, up-to-date, provide excellent illustrations and contain few editorial mistakes. Overall, this book is for specialists who are interested in specific aspects of insect flight. The authors selected for this overwhelming task were well chosen and are leaders in their respective areas. Some of the topics presented have been covered by the same authors elsewhere; however, they all have updated the information and presented new ideas.

I am taking the privilege to list all the chapters presented and the respective authors. The reasons for doing this are twofold: cost and specialization. Because of the exorbitant price (i.e. $195 U.S., $225 outside U.S.) for the 371 pages, I strongly recommend that individuals interested in just one or a few chapters contact a wealthy friend for a loaner or, for most of us (i.e. either poor or not having wealthy friends), have the library order it. The only glaring weakness of the book, despite its cost, is the last two chapters. The authors of Chapt. 14 make the following statement on p. 322: "Our objective in this chapter is to describe the present state of insect control, considering its failures as well as its successes, because it is only by taking this 'warts and all' approach that we can realistically set the scene for an analysis of future requirements." The authors completed this objective, even if it is disjointed from the rest of the book. The final decision to make sure that all the chapters of a book somehow relate to the theme of the book lies with the editors and here they failed. Not only did they fail to recognize that this chapter, as written, did not fit well into this volume, but they missed an excellent opportunity to stress the importance of flight to current and future control strategies. I am sure the editors initially recognized the importance of including a chapter that would integrate these two topics, otherwise they wouldn't have included it in the volume. They could have discussed such topics as dispersion, flight capabilities of different pests, founder effects on resistance management strategies, passive flight of certain vectors (i.e. aphids) of plant diseases and their dependence on prevailing winds, and effect(s) parasite loads may have on flight in medically important species. Chapt. 15, by the same authors as Chapt. 14, again met the stated objective of the authors but failed to hit the target. Its presence, however, in a treatise that is mainly biased towards basic research should serve an important function. Chapt. 14 provides the novice with an excellent overview of future control strategies. Maybe, and just maybe, individuals interested in the more basic aspects of flight biology will read it. If they do, and I strongly recommend that they do, they should attempt to relate how their

area of interest in insect flight relates to improving control strategies. I am sure that this type of synthesis is what the editors wanted to promote when they decided to include these last two chapters.

This reviewer recommends you treat this book as a buffet: only take those dishes that interest you. Following is the menu: Chapt. 1. Mechanics and Aerodynamics of Flight—W. Nachtigall, pp. 1–29; Chapt. 2. Structure and Function in Flight Muscle—D. J. Aidley, pp. 31–49; Chapt. 3. Development of the Flight Motor Pattern—Wolfram Kutsch, pp. 51–73; Chapt. 4. Sense Organs and the Control of Flight—Bernhard Möhl, pp. 75–97; Chapt. 5. The Evolution and Significance of Migratory Flight—Hugh Dingle, pp. 99–114; Chapt. 6. Genes, Environment, and Insect Flight—A. G. Gatehouse, pp. 115–138; Chapt. 7. Hormonal Control of Flight—Mary Ann Rankin, pp. 139–163; Chapt. 8. Swarm Flight Behavior in Flies and Locusts—Richard John Cooter, pp. 165–203; Chapt. 9. Orientation and Foraging in Honeybees—Fred C. Dyer and Thomas D. Seeley, pp. 205–230; Chapt. 10. Pheromones and Flight Behavior—T. C. Baker, pp. 231–255; Chapt. 11. Oxygen Consumption During Flight—Timothy M. Casey, pp. 257–272; Chapt. 12. Mobilization and Transport of Fuels to the Flight Muscles—Colin H. Wheeler, pp. 273–303; Chapt. 13. Utilization of Fuels by the Flight Muscles—D. J. Candy, pp. 305–319; Chapt. 14. Problems in the Control of Flying Insect Pests—D. P. Giles and A. R. Jutsum, pp. 321–336; Chapt. 15. Prospects for Better Control Strategies—A. R. Jutsum and D. P. Giles, pp. 337–371.

Reviewed by John G. Stoffolano, Jr., *Department of Entomology, Fernald Hall, University of Massachusetts, Amherst, Massachusetts 01003.*

PROC. ENTOMOL. SOC. WASH.
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Society Meetings

954th Regular Meeting—January 4, 1990

The 954th Regular Meeting of the Entomological Society of Washington was called to order by President Jeffrey R. Aldrich in the Naturalist Center, National Museum of Natural History, at 8 p.m. on 4 January 1990. Twenty-two members, two guests and a joker were present. Minutes of the December meeting were read and approved.

Membership Chairman G. B. White read the names of the following applicants for membership: James M. Hill, Natural Resources Division, Maryland-National Capital Park and Planning Commission, Chevy Chase; Roberta ("Bobbe") Krueger, Haymarket, Virginia; Timothy George Myles, Department of Entomology, University of Arizona, Tucson; and David H. Young, Waltham, Massachusetts.

President Aldrich reviewed the results of the Executive Committee meeting held earlier in the day. The Committee has decided to hold our Regular Meeting for May in the Visitors Center (or "Log Lodge") at the Beltsville Agricultural Research Center. Tentative plans for this event include talks by a number of entomologists belonging to the Agricultural Research Service. The Executive Committee also noted that our annual donation of $750 to the American Association for Zoological Nomenclature is now a routine feature of ESW budgets (Proc. Entomol. Soc. Wash. 91: 651, 653, October 1989) but that the nation's largest entomological organization, the Entomological Society of America, has refused to support the AAZN, ostensibly because all such contributions must be approved by the entire ESA membership. However, it is well known that there is pressure within ESA to bring this matter to a vote, and Dr. Aldrich suggests that our Society can encourage a favorable outcome by publishing a letter of challenge in either the ESA *Newsletter* or *Bulletin*.

Doug Sutherland circulated a notebook containing letters from the American and North Carolina entomological societies supporting the selection of the monarch butterfly, *Danaus plexippus* (Linnaeus), as our national insect.

R. G. Robbins thanked J. M. Kingsolver for providing the Smithsonian's Acarology Unit with a recent listing of 139 references on Lyme disease produced through the *Quick Bibliography Series* of the National Agricultural Library (NAL-BIBL. QB 89-87). All bibliographies in this series are derived from searches of the AGRICOLA database and can be obtained by writing to the NAL, Public Services Division, Room 111, Beltsville, Maryland 20705.

The speaker for the evening was our Past President, F. Christian Thompson, Systematic Entomology Laboratory, U.S. Department of Agriculture, whose talk was entitled "Will Systematics Survive the 21st Century?" Dr. Thompson is pessimistic, in part because entomology, like other branches of natural science, has suffered a certain loss of identity in recent decades; in part also because systematists are often their own worst enemies, lending credence to the view that they are just esoteric academics; but largely because taxonomists across the board are so intransigently conservative, refusing to adapt to, let alone take advantage of, technological advances that could automate their workplaces, save them countless thousands of hours, and even elevate their profession in the eyes of the nonsystematic scientific community. Given the immensity of the systematist's task—that of generating and disseminating biosystematic information—and the presumably permanent paucity of funds, space and personnel, there is no question that automation is the key to survival. But in any such scheme, systematists are the bottleneck, so their modus operandi must be to divert some of the avalanche of data from themselves while

increasing the rate of data flow. In a word: computerize! Presently, a relational database model for biosystematic information is being developed by Dr. Thompson and several colleagues. This and other expert systems will use names of taxa, characters, attributes, and certain comments (e.g. geography, season) to generate biosystematic information with unsurpassed speed and flexibility. Over time, the volume of this information can be further condensed via CD ROM technology.

Mignon Davis thanked Rose Ella and Ted Spilman for providing this evening's treats. Visitors were introduced and the meeting was adjourned at 9:20 p.m.

Richard G. Robbins, *Recording Secretary*

955th Regular Meeting—February 1, 1990

The 955th Regular Meeting of the Entomological Society of Washington was called to order by President Jeffrey R. Aldrich in the Naturalist Center, National Museum of Natural History, at 8:08 p.m. on 1 February 1990. Fifteen members and 15 guests were present. Minutes of the January meeting were read and approved.

Recording Secretary R. G. Robbins read the names of the following applicants for membership: Ralph P. Eckerlin, Division of Natural Sciences, Northern Virginia Community College, Annandale; Terry A. Wheeler, Department of Environmental Biology, University of Guelph, Ontario, Canada; and Jing Zhai, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg.

Mignon Davis circulated a sign-up sheet for volunteers to bring refreshments to our meetings.

President Aldrich recounted a recent meeting with Jean Boek, President of the Washington Academy of Sciences, who disclosed that he is being impeached! Because our Society is a member of the Academy, Dr. Aldrich has decided not to hobnob with that organization's mutineers, who allegedly are headquartered at George Washington University. President Aldrich also announced that he had met with a realty specialist at the Beltsville Agricultural Research Center, who informed him that as of this March we will be required to pay a yearly fee of approximately $4.30 per square foot for the storage of back issues of the *Proceedings* and other Society publications on reservation grounds. Since the shelf space required for our present backlog is estimated to be no less than 200 square feet, we will soon be facing an insufferable annual assessment of almost $900. A discount sale is probably inevitable, but Dr. Aldrich appealed to the membership for additional means of drastically reducing this literary logjam.

W. E. Bickley displayed a winsome new book for insect enthusiasts, *Ninety-nine Gnats, Nits, and Nibblers,* by May R. Berenbaum, 1989, University of Illinois Press, Urbana and Chicago, xxi + 254 + 9 pages, illustrated, $29.95/cloth (ISBN 0-252-01571-1), $9.95/paper (ISBN 0-252-06027X).

R. P. Eckerlin exhibited two specimens of the squirrel flea *Orchopeas howardi* (Baker) (Siphonaptera: Ceratophyllidae) that had been found on a child. Radioecological studies of the population dynamics of this flea have been conducted in Virginia, where *O. howardi* has been implicated as a potential vector of sylvan epidemic typhus (*Rickettsia prowazekii*), although experimental attempts to induce transmission by biting have been unsuccessful (Sonenshine et al. 1978, Amer. J. Trop. Med. Hyg. 27: 339–349; Bozeman et al. 1981, Amer. J. Trop. Med. Hyg. 30: 253–263).

Edd Barrows circulated two breathtaking guides to the entomological exhibits at the Staatliches Naturhistorisches Museum in Braunschweig, Federal Republic of Germany, *Insekten: Begleitheft zum Insektensaal,* by Jürgen Hevers (ISBN 3-925538-00-3), and *Insekten und Spinnen aus Edelstahl Plastiken,* by Hans Jähne and Jürgen He-

vers (ISBN 3-7682-1393-5). Though lavishly illustrated and printed on glossy paper, both guides can only hint at the elegance of the treasures on view in this small museum, which encompasses *Taxonomie, Morphologie, Schutztrachten zum Überleben* (camouflage), *staatenbildende Insekten* (social insects), and *Insekten im Wald und der Wasseroberfläche* (forest and aquatic insects). At the time of Dr. Barrows' visit (August 1989), the museum also contained a living colony of *Honigbienen,* all hard at work in the best German tradition.

Ed Saugstad exhibited one end of a towel rack that had been made from an Asian hardwood but, apparently unbeknownst to the manufacturer, rendered hollow by the borings of cerambycid larvae.

The speaker for the evening was M. Alma Solis, Systematic Entomology Laboratory, U.S. Department of Agriculture, whose talk was entitled "Contributions of Annette Braun, an Early 20th Century Microlepidopterist." One of the pioneer students of North American leaf-mining Lepidoptera (a vast assemblage of some 16 families comprising over 335 species), Annette Frances Braun is chiefly remembered for her large monographic works. Her Ph.D. dissertation at the University of Cincinnati in 1912 focused on the evolution of color pattern in the gracilariid genus *Lithocolletis* Hübner, but in this and subsequent papers the careful reader will discern seminal concepts of homology and outgroup comparison that presaged modern phylogenetic methods. In later life, Miss Braun produced revisions of the North American Elachistidae and Tischeriidae, as well as the lyonetiid genus *Bucculatrix* Zeller; all were published as *Memoirs* of the American Entomological Society. Together with her sister Lucy (a famous botanist), she was an early advocate of habitat conservation. A long-overdue tribute to this kind, sedulous scientist will be published by Dr. Solis in the summer 1990 issue of *American Entomologist* (formerly the *Bulletin* of the Entomological Society of America).

Our numerous visitors were introduced and the meeting was adjourned at 8:55 p.m. Refreshments followed.

Richard G. Robbins, *Recording Secretary*

956th Regular Meeting—March 1, 1990

The 956th Regular Meeting of the Entomological Society of Washington was called to order by President Jeffrey R. Aldrich in the Naturalist Center, National Museum of Natural History, at 8 p.m. on 1 March 1990. Fifteen members and 10 guests were present. Minutes of the February meeting were read and approved.

Membership Chairman G. B. White read the names of the following applicants for membership: William A. Bruce, Stephen Hight, and Walter S. Sheppard, all U.S. Department of Agriculture, Agricultural Research Service, Beneficial Insects Laboratory, Beltsville, Maryland; Ernie May, Snow Entomological Museum, University of Kansas, Lawrence; Richard L. Orr, College Park, Maryland; Michael P. Parrella, Department of Entomology, University of California, Davis; and Kurt L. Schmude, Department of Entomology, University of Wisconsin, Madison. Chairman White also announced the establishment of the Anne M. Wieber Memorial Fund, in honor of our late Custodian. Begun in the closing months of 1989 and spearheaded by Gaye L. Williams, Maryland Department of Agriculture, the Fund currently contains about $400, all of which will be used to purchase books on insects for the Naturalist Center, National Museum of Natural History. Certainly, this is a cause worthy of espousal by the entire ESW membership, which greatly benefited from Anne's selfless dedication. Checks in any amount should be made payable to the Naturalist Center and sent to either Chairman White or Ms. Williams.

President Aldrich again solicited ideas for reducing the Society's backlog of unsold *Proceedings* and other publications. A new storage facility has been located, but it will

accommodate only about half our present holdings. Dr. Aldrich suggested that authors of *Memoirs* and miscellaneous publications could do the Society a service by personally taking responsibility for surplus stock.

James M. Hill, Ecologist, Maryland-National Capital Park and Planning Commission, exhibited a bag of belostomatids that he had purchased in the frozen food section of an Oriental supermarket in downtown Silver Spring. An aficionado of Thai cookery, Mr. Hill observed that these rapacious aquatic bugs are standard fare in Southeast Asia and invited those present to try some samples. A male specimen examined by P. J. Spangler, Department of Entomology, Smithsonian Institution, was assigned to the genus *Lethocerus*, which includes some of the world's largest Hemiptera. Several specimens bore the calyptostases of hydrachnidian larvae (Acari: Acariformes: Actinedida), which commonly parasitize aquatic and semiaquatic insects.

President Aldrich recounted his recent trip to Brazil in search of stink bugs. Among his finds were the predaceous pentatomid *Stiretrus erythrocephalus* (Lepeletier and Serville) and its curiously similar prey, the chrysomelid beetle *Phaedon* sp. near *confinis* Klug. Striking similarity between predator and prey suggests aggressive mimicry but other interpretations are possible. Specimens of both bug and beetle were exhibited to the membership.

R. G. Robbins displayed a new dictionary for entomogermanophiles: *Wörterbuch für Veterinärmedizin und Biowissenschaften*, compiled by Roy Mack, published in 1988 by Paul Parey, Berlin and Hamburg, 321 pages, $35.00/paper, ISBN 3-489-50516-6. Though not intended as a replacement for the classic De Vries dictionary, which is out of print and will not be republished, this work largely fills the gap by focusing on technical terms in the fields of anatomy, microbiology, physiology, parasitology, pathology, pharmacology, toxicology, and systematics. Besides the usual German-English and English-German sections, the dictionary contains an appendix of Latin anatomical and medical terms together with their German and English equivalents. Two additional appendices provide the German and English common names of animals (e.g. *Bombyx mori*, De: Seidenraupe, En: silkworm) and plants (e.g. *Papaver somniferum*, De: Schlaf-Mohn, En: opium poppy). In the United States, orders for this invaluable reference should be sent to Paul Parey Scientific Publishers, 35-37 West 38th Street, No. 3W, New York, NY 10018.

The speaker for the evening was Susan J. Weller, Smithsonian Fellow, Department of Entomology, whose talk was entitled "Why are Notodontid Genitalia so Variable—Sexual Selection?" Males of Neotropical notodontids belonging to the tribe Nystaleini possess a number of novel courtship structures, the most spectacular of which is a more or less elaborate modification of the external genitalia: the lower portion of the valve, the sacculus, contains glandular material, and androconial scales are attached to its pleated, membranous base. In the relatively large *Nystalea* clade, which includes nearly 200 species, all males possess these valve scent organs as well as secondary scent organs on either the legs or abdomen. By contrast, the *Dasylophia* clade comprises just 55 species, only one genus possesses an abdominal courtship structure, and the valve scent organs are reduced or lost. Such differences are consistent with the theory of sexual selection via female choice. In the *Nystalea* clade, chemical communication may allow for rapid divergence of signals driven by female choice, thereby promoting speciation. However, in the *Dasylophia* clade, mechanical communication through genitalic contact is the only means available for females to assess different males. Either female choice does not occur in the *Dasylophia* clade or morphological structures cannot evolve as quickly as chemical signals. Dr. Weller illustrated her fluent presentation with slides of some striking no-

todontid larvae, including the lobster moth, *Stauropus fagi* Linnaeus, and a spider mimic, *Cnethodonta grisescens* Staudinger. She also exhibited the eminently perusable text *Sexual Selection and Animal Genitalia*, by William G. Eberhard, Harvard University Press, cloth edition 1985, 288 pages, $26.00, ISBN 0-674-80283-7; paper edition 1988, 256 pages, $14.95, ISBN 0-674-80284-5.

President Aldrich thanked Bill Bickley and Edd Barrows for supplying this evening's genteel repast of Girl Scout cookies and soft drinks. Visitors were introduced and the meeting was adjourned at 9 p.m.

Richard G. Robbins, *Recording Secretary*

957th Regular Meeting—April 5, 1990

The 957th Regular Meeting of the Entomological Society of Washington was called to order by President Jeffrey R. Aldrich in the Naturalist Center, National Museum of Natural History, at 8 p.m. on 5 April 1990. Sixteen members and nine guests were present. Minutes of the March meeting were read and approved.

President Aldrich read the name of tonight's guest speaker (*vide infra*), who has applied for membership.

President-Elect David R. Smith announced that the annual joint banquet of the Entomological Society of Washington, Pest Science Society of Washington, and Maryland Entomological Society will be held on the evening of 7 June in the Associates Court, National Museum of Natural History. This year's Master of Ceremonies will be Douglas W. S. Sutherland, Entomologist, U.S. Environmental Protection Agency. Our after-dinner speaker will be David A. Nickle, Research Entomologist, Systematic Entomology Laboratory, U.S. Department of Agriculture, who will regale us with an audio-visual presentation entitled "Hide and Sing in the Rainforest: the Katydids of the Peruvian Amazon."

President Aldrich reminded the membership that our Regular Meeting for May will be held in the National Visitors Center (or "Log Lodge") at the Beltsville Agricultural Research Center. He also announced that on 11 April the Center for Agricultural Biotechnology and the Department of Entomology, University of Maryland, College Park, will co-sponsor a special seminar entitled "Mating Systems in Ghost Moths (Hepialidae) and other Primitive Lepidoptera: Role Reversal, Sex Scaling, and Contingency Analyses," presented by David L. Wagner, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs. Dr. Wagner's data suggest that basal lineages of Lepidoptera and Trichoptera possessed a female-released, long-range sex attractant and that the unusual male-based calling systems found in the Hepialidae represent one or more special derivations. The morphological diversity and taxonomic distribution of male scent scales (androconia) have been examined in several clades and appear to be the most rapidly evolving adult structures. Explanations of this evolutionary lability will be explored, with emphasis on the use of statistical correlation analyses, which treat species as independent data points.

At the request of Bill Bickley, Rich Robbins read an announcement from Towson State University, which will host the 51st annual meeting of the Association of Southeastern Biologists (ASB), 18–21 April, in Baltimore. Societies meeting in conjunction with the ASB include Beta Beta Beta; the Botanical Society of America, Southeastern Section; the Ecological Society of America, Southeastern and Washington, D.C., Chapters; the Society of Wetlands Scientists, Northeastern and South Atlantic Chapters; and the Southern Appalachian Botanical Club. Field trips are planned to such nearby attractions as Fort McHenry, the McCormick Spice Company, and the National Aquarium in Baltimore, as well as to the Beltsville Agricultural Research Center, the Patuxent Wildlife Research Center, Soldiers Delight Serpentine Area, the Smithsonian

Environmental Research Center on the Rhode River south of Annapolis, and Longwood Gardens in southeastern Pennsylvania. Registration, paper and poster presentations, exhibits, and general sessions will be held at the Lord Baltimore Radisson Plaza, about 10 miles south of the Towson State campus. ASB membership is not required for registration.

D. R. Smith exhibited a lavish new publication on what are probably the world's most ubiquitous insects, *The Ants,* by Bert Hölldobler and Edward O. Wilson, 1990, published by the Belknap Press of Harvard University Press, Cambridge, Massachusetts, xiv + 732 pages, ISBN 0-674-04075-9, $65.00/cloth (alkaline paper). A large page format, numerous full-color paintings, and an illustrated key to the approximately 300 recognized ant genera make this authoritative but engrossing volume a "must buy" for any entomologist, regardless of specialization.

T. J. Spilman displayed an attractive new paperback, *Nymphs of the Sahelian Grasshoppers: An Illustrated Guide,* by G. B. Popov, 1989, published by the Overseas Development Natural Resources Institute, Chatham, Kent, United Kingdom, with partial funding from the U.S. Agency for International Development, v + 158 pages, ISBN 0-85954-264-5. Though small enough to slip into a pocket, this book succeeds in illustrating with color drawings and photographs one or more instars of some 78 species of "hoppers" from the vast sub-Saharan semidesert known as the Sahel. Associated symbols provide instant summaries of life cycles, food and habitat preferences, maximum number of generations per year, number of instars by sex, gregariousness, infraspecific variation and, of course, economic importance. Common names appear in both English and French, a reflection of this region's equally colorful colonial history.

President Aldrich projected slides of the spined soldier bug, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), an efficient springtime predator of lepidopterous larvae. He also distributed samples of this species' aggregative pheromone, formulated into small, gumball-like spheres for shotgun distribution.

The speaker for the evening was Timothy P. Friedlander, Center for Agricultural Biotechnology, University of Maryland, whose talk was entitled "Moths and Molecules: Reconstructing a Phylogeny from Nucleic Acid Sequence Data." Molecular systematics is a useful tool in taxonomic situations where there are many species but few morphological characters. While at Louisiana State University, Dr. Friedlander attempted to construct a phylogeny of the superfamilies of higher Lepidoptera, infraorder Ditrysia, by comparing ribosomal RNA (rRNA) sequence data among 35 representative species. Taxonomic characters from rRNA sequences were shown to be various kinds of nucleotide base substitutions, including transitions, transversions, and insertion/deletion events. Sequence characters were evaluated for homology and independence, after alignment, by looking at secondary structure, and relative frequency classes were assessed. The software package Phylogenetic Analysis Using Parsimony (PAUP) was chosen for evolutionary hypothesis construction. Characters of the less frequent character classes were analyzed, these being more appropriate to such inference. Taxa were chosen with the goal of estimating the hypothetical ancestral character states for each independent superfamily; this method reduces both the number of taxa in a computer run and the amount of homoplasy—without reducing the number of characters. Dr. Friedlander's molecular analysis of the Ditrysia yielded some unexpected results: butterflies did not group with other macrolepidopterans, while lasiocampids grouped strongly with cossids and castniids rather than with other bombycoids.

Edd Barrows projected a series of slides

from last year's annual banquet, including one of the irrepressible Doug Sutherland sporting a plexippian bow tie.

Don Davis thanked his daughter Marisa for providing this evening's "onion bread and horseradish dip." Visitors were introduced and the meeting was adjourned at 9 p.m.

Richard G. Robbins, *Recording Secretary*

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Cynipid Galls of the Southwest, by Lewis H. Weld	3.00
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A Short History of the Entomological Society of Washington, by Ashley B. Gurney	1.00
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Memoirs of the Entomological Society of Washington

No. 1.	The North American Bees of the Genus *Osmia*, by Grace Sandhouse. 167 pp. 1939	$15.00
No. 2.	A Classification of Larvae and Adults of the Genus *Phyllophaga*, by Adam G. Boving. 95 pp. 1942	(out of print)
No. 3.	The Nearctic Leafhoppers, a Generic Classification and Check List, by Paul Wilson Oman. 253 pp. 1949	15.00
No. 4.	A Manual of the Chiggers, by G. W. Wharton and H. S. Fuller. 185 pp. 1952	15.00
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No. 6.	The Female Tabanidae of Japan, Korea and Manchuria, by Wallace P. Murdoch and Hirosi Takahasi. 230 pp. 1969	15.00
No. 7.	Ant Larvae: Review and Synthesis, by George C. Wheeler and Jeanette Wheeler. 108 pp. 1976	11.00
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. 9.	The Flower Flies of the West Indies (Diptera: Syrphidae), by F. Christian Thompson. 200 pp. 1981	10.00
No. 10.	Recent Advances in Dipteran Systematics: Commemorative Volume in Honor of Curtis W. Sabrosky. Edited by Wayne N. Mathis and F. Christian Thompson. 227 pp. 1982	11.00
No. 11.	A Systematic Study of the Japanese Chloropidae (Diptera), by Kenkichi Kanmiya. 370 pp. 1983	18.00
No. 12.	The Holarctic Genera of Mymaridae (Hymenoptera: Chalcidoidae), by Michael E. Schauff. 67 pp. 1984	5.00
No. 13.	An Identification Manual for the North American Genera of the Family Braconidae (Hymenoptera), by Paul M. Marsh, Scott R. Shaw, and Robert A. Wharton. 98 pp. 1987	18.00

Back issues of the Proceedings of the Entomological Society of Washington are available at $25.00 per volume to non-members and $13.00 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, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560.

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